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Corrections for Volume II

The legends under the figures on pages 83 and 86 should be reversed The figure on 83 should have the legend appearing on page 86 and should be numbered 3 the figure on page 86 should have the legend appearing on page 83 and should be numbered 2

Instead of Map showing area surveyed" the following legend should appear under the map on page 110

Distribution of the varieties of *Juncus effusus* in the state of Washington and vicinity circles var *pacificus* squares var *brunneus* triangles var *gracilis* star var *caeruleomontanus*

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CYTOLOGY OF TRITICUM, SECALE, AND AEGILOPS HYBRIDS WITH REFERENCE TO PHYLOGENY[2]

HANNAH C AASE

(Received for publication March 3 1930)

I MATERIALS AND METHODS

The hybridizations were accomplished in the cereal nursery of the Washington Agricultural Experiment Station under the direction of Dr E F Gaines The writer expresses hearty appreciation of the splendid material so generously made available for this study, and thanks Dr Gaines, especially, for his enthusiastic cooperation and interest in these investigations

The anthers and pistils were collected from plants grown in the botany greenhouse and the cereal nursery The collecting season in Pullman usually begins in March with greenhouse material, and ends in the latter part of August with the field material Pollen mother cells were examined by Belling's iron-aceto-carmine method during the growing season The paraffin material was killed in modifications of Bouin's fluid, acetic acid-alcohol 1-3, Nawashin's fluid, or Nawashin's preceded by a minute or more immersion in acetic acid-alcohol The sections were cut 15-18 microns in thickness and stained in Heidenhain's iron-alum hæmatoxylin, or in a few cases by modifications of Newton's iodine-gentian violet The latter gave fine results if preceded by a killing reagent containing chromic acid or a few minutes immersion of slides in one per cent aqueous solution of chromic acid

Differential staining occurred in some cases both in iron-aceto-carmine (Fig 2 D) and in hæmatoxylin (Fig 4, Fig 10 E)

All drawings were made by the aid of the camera lucida In most cases the entire pollen mother cell has been represented Some ovules were sectioned in such a manner that the chromosomes of the embryo sac mother cell appeared in two sections Some of these ovules have been drawn and the smaller group of chromosomes has been superimposed upon the section containing the larger group This, however, has been done only when the observer was absolutely certain of the correctness of the observation, and in all cases the superimposed chromosomes are unshaded, for although great care has been exercised, the position of the superimposed chromosomes must necessarily be only approximately correct

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[2] Contribution from the Department of Botany State College of Washington No 25

The cytological account is confined to the meiotic phases in the pollen mother cells and embryo sac mother cells of F_1 hybrids and in some cases their parents As ovules have heretofore been less frequently represented in cytological accounts in cereals, special effort has been made to compare the chromosome behavior in ovules and anthers when both have been available on the slides

Chromosome conjugation particularly has been recorded, and correlated with types of pollen grains and ovule tetrads formed Two general types of chromosome conjugation occur One will be referred to as the closed type and represents the state in which the two members of a synaptic pair are connected to each other at both ends The closed type predominates in the meiosis of an apparently stable species, or whenever members of a pair are definitely homologous The second type will be referred to as the open type, and represents the condition in which the two members of a synaptic pair are connected to each other at one end only This type may be found in all the wheat Aegilops, and rye parents studied by the writer, but comparatively infrequently, and least frequently in those that suggest themselves as the more primary species such as Einkorn (Table 10) A high percent of the open type will be assumed to indicate decreased attraction between homologous mates

The hybrids will for convenience be grouped according to their somatic chromosome number as triploids, tetraploids, and pentaploids The polyploidy suggested by these terms refers to the multiplication of the number 7 without implying close chromosome homology between sets of 7 It is the indication of such homology between chromosome sets that will be most carefully noted in the hybrids investigated It is possible that such indications may offer a clue to the chromosome history and hence phylogenetic relationships in 28- and 42-chromosome wheats and Aegilops In other words, the study of chromosome homology may be one feasible method of discovering whether the chromosome complement of each of these plants is actually constructed by the multiplication of a specific 7-chromosome block, or by the addition of more or less dissimilar 7-chromosome blocks, and finally of discovering the original source of each block

The delusiveness of this method is on a par with that of any other method yet devised, when used alone The satisfactory solution of the problem will, no doubt, require a comparison of results obtained through several methods

The hexaploid wheats will in general be referred to as vulgare or the vulgare group, the tetraploid wheats as emmer or the emmer group, and the diploid wheats as einkorn or the einkorn group

The data compiled in tables 1-9 have in the majority of cases been obtained from direct statements appearing in the published reports by the respective investigators, in a few instances by summarizing tabulated reports, and have rarely been supplemented by interpretation of illustrations To avoid misquotations, interrogation-points have been used to indicate uncertainty as to the exactness of the writer's interpretation of the data given by the investigator quoted

II TRIPLOIDS

(a) *Wheat Triploids*

TABLE 1 NUMBER OF BIVALENTS IN WHEAT TRIPLOIDS

Hybrid	Range	Mode	Author	Year
T monococcum Hornemanni (7) x *T turgidum pseudo cervinum* (14)	5(?)-7	7	Sax	1922
T dicoccum (14) x *T monococcum* (7)	4 7	-	Kihara	1924
T aegilopoides (7) x *T dicoccum* (14)	4-7	-	"	"
T monococcum (einkorn) (7) x *T turgidum* var *buccale* (14)	3 7	5 6	Thompson	1926
T dicoccoides x *T aegilopoides*	0-5	-	Bleier	1930
T durum (Kubanka) (14) x *T monococcum* (Einkorn) (7)	4-7	6	Aase	1930
T dicoccoides (Wild Emmer) (14) x *T monococcum* (Einkorn)	4-7	5 6	"	1930

The several reports on chromosome conjugation in triploid wheat hybrids show rather close agreement in view of the fact that each investigator is dealing with a different variety, and in most cases a different species, as one of the parents (Table 1) Decreasing affinity of pairing mates is indicated by the small number of pairs in many cells, and is evidenced still further by the large proportion of open pairs (Fig 4 and Table 10) reported or illustrated by all the investigators *T monococcum* x *T turgidum* var *buccale,* described by Thompson, and *T dicoccoides* x *T aegilopoides,* described by Bleier, show the largest proportion of open pairs as well as the smallest number of total pairs while *T monococcum* x *T turgidum* var *pseudo-cervinum* described by Sax shows the opposite extremes in these respects

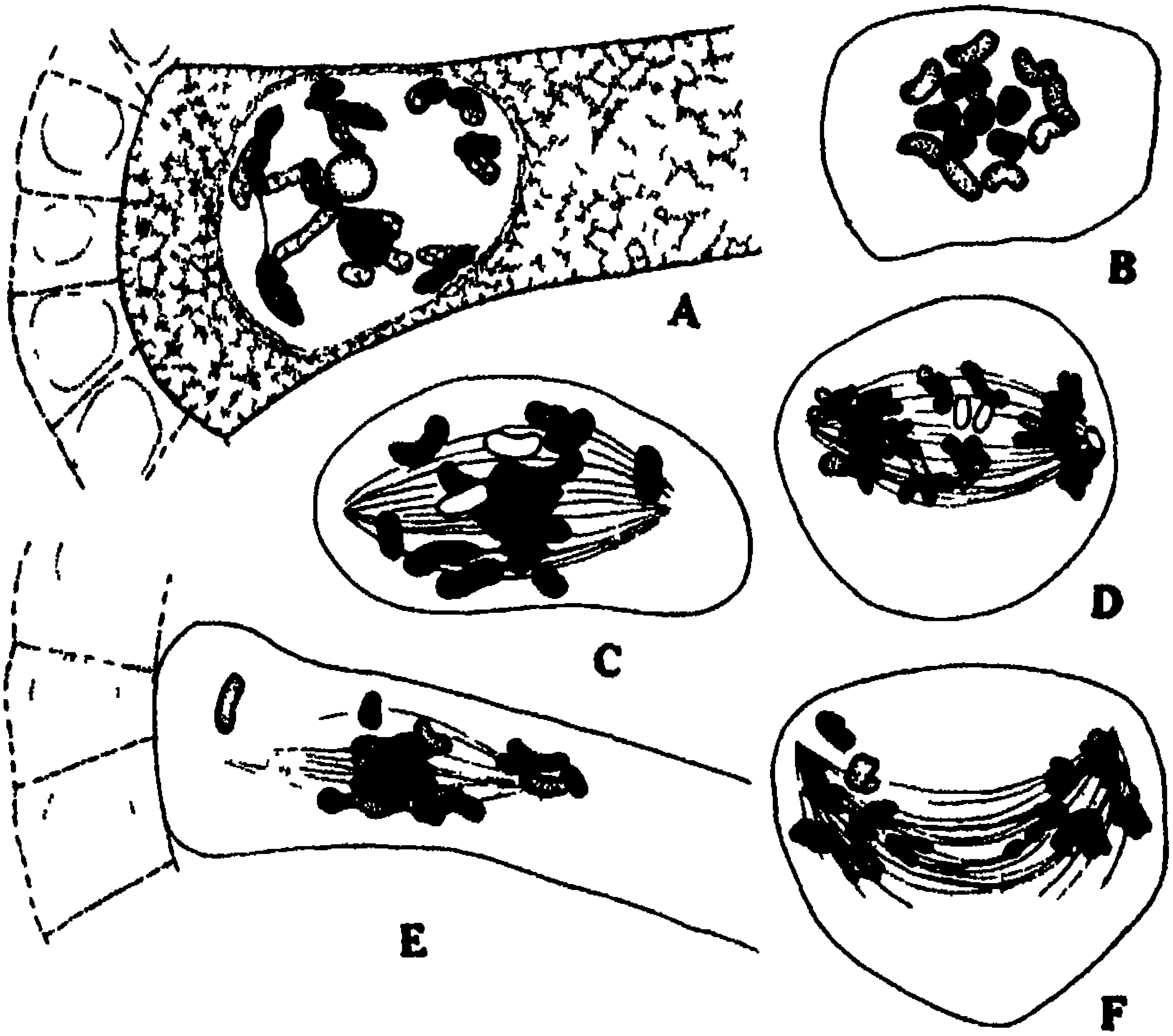


Fig 1 Wheat Triploids first meiotic division Triticum dicoccoides (14) x T monococcum (7) A diakinesis in megaspore mother cell 9 univalents and 4 open and 2 closed bivalents in evidence B polar view 6 bivalents and 9 univalents C 4 closed and 1 open bivalents 1 trivalent and 8 univalents D anaphase All univalents have split but actual division affects only those lying in center of spindle

T durum (14) x T monococcum E megaspore mother cell 5 closed and 1 open bivalents and 9 univalents F more advanced stage than D X 1800

In *T dicoccoides* x *T monococcum* trivalents appear at the rate of one in 5 cells (Table 10) In *T dicoccum* x *T monococcum* and *T* *aegilopoides* x *T dicoccum* Kihara and Nishiyama (1928) observed pollen mother cells containing as many as three trivalents, and suggest that chromosomes from the B group in Emmer conjugate with chromosomes of the A group to form trivalents All trivalents illustrated by these investigators, as well as those observed by the writer are of the V or open type (Fig 1 C and Fig 4)

The bivalents of whichever type and the trivalents extend through the equatorial plate The univalents are usually scattered over the spindle (Fig 1 C E) but may lie approximately at the plate, thus encircling the bivalents (Fig 1 B) The few ovules caught in meiotic phases (Fig 1 A, E) show the same type of chromosome orientation and conjugation as the anthers

During the anaphase the bivalents disjoin and migrate to the poles as described also by other investigators The procedure in respect to the univalents in the first division seems to be to a great extent determined by their location on the spindle at the time the equational split begins Usually the equational split of the univalents becomes evident as the members of the bivalents are migrating to the poles The equational split occurs simultaneously in all the univalents as well as in the disjoined members of the bivalents

The number of univalents that will actually divide, depends on the number lying at the equatorial plate position at the time the equational split occurs (Fig 1 D, F) The two members of a split univalent lying off the equatorial plate go together to the nearest pole There is some indication of the movement of univalents to the equatorial position following the disjunction of the bivalents but evidently not as definite as in Thompson's material in which "After the bivalents have divided all the univalents arrange themselves at the equator in strikingly regular fashion, and each divides equationally" Kihara observed both divided and undivided univalents migrating to the poles Sax observed only undivided univalents at the first division

The pollen tetrads are comparatively regular (Fig 5 B, F) and the pollen grains of even size (Fig 5C, G) Micronuclei representing one or two chromosomes each are often present in both Tetrad formation in the ovule is comparatively regular (Fig 5 A, D, E) In some the second division is delayed in the outer cell of the diad

(b) *Wheat-rye Triploid*

The general meiotic procedure in the wheat-rye triploid, *T durum* (Kubanka) (14) x *S cereale* (Rosen) (7), is very similar to that of the tetraploid *T vulgare* (Triplet) (21) x *S cereale* (Rosen) In both hybrids there is a bivalent of the open type in slightly more than half of the pollen mother cells In the triploid a maximum of 4 such bivalents has been observed, in the tetraploid 3 No trivalents have been found in the triploid and only a trace in the tetraploid (Table 10)

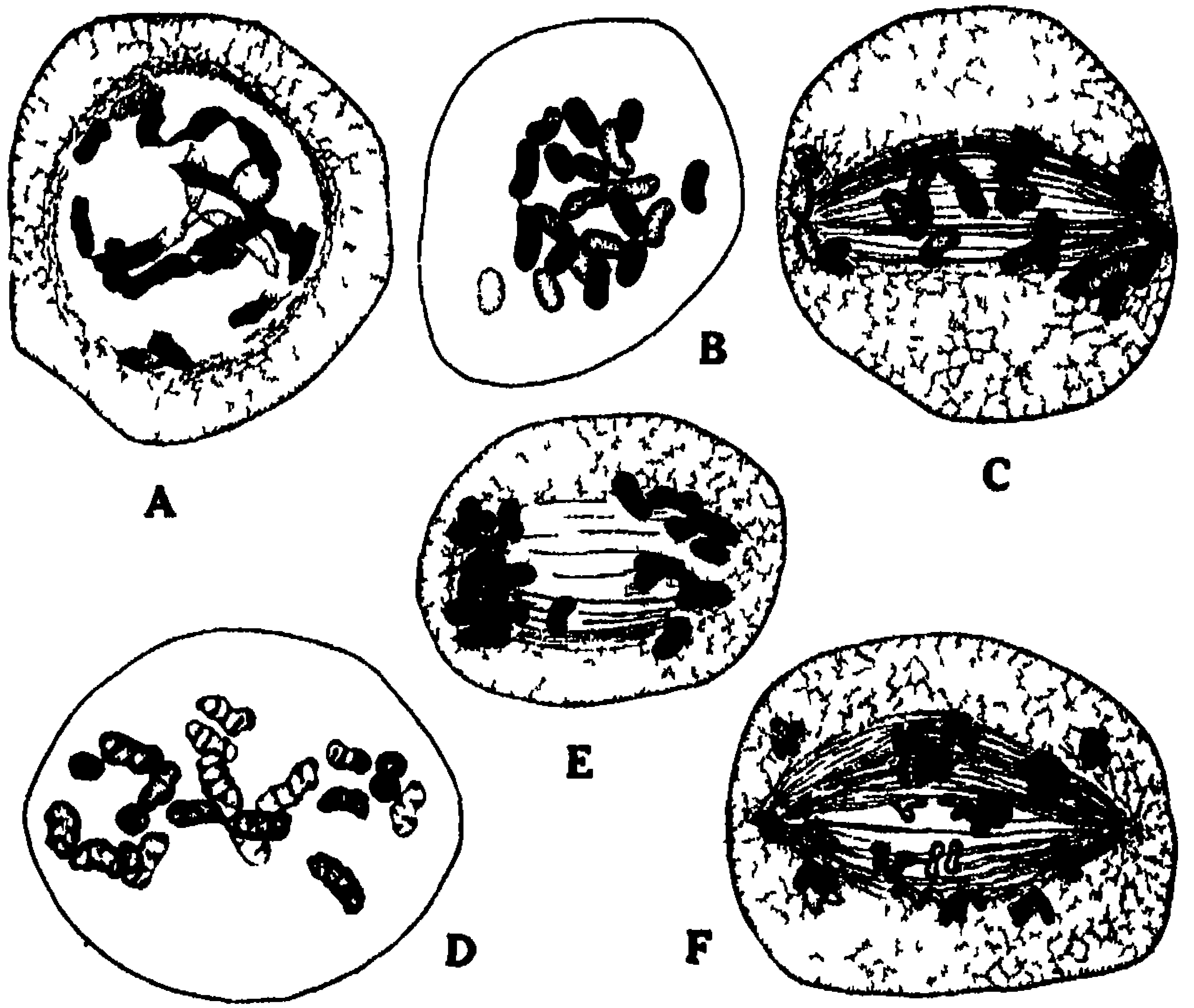


Fig 2 Wheat rye triploid first meiotic division Triticum durum (14) x Secale cereale (7) A late prophase some univalent chromosomes attached end to end B early metaphase 21 univalents C metaphase typical distribution of univalents through the entire spindle *D* metaphase 1 open bivalent and 19 univalents Differential staining sometimes observed (iron aceto carmine) E anaphase 10 univalents approaching one pole and 11 the other pole F anaphase Splitting of the univalents occurs before migration to the poles Univalents lying at the region of the normal equatorial plate will divide X 1800

The late prophase in figure 2 A of the triploid shows the end-to-end attachment of the chromosomes All or nearly all of these connections will vanish, leaving practically only univalents in contrast to figure 1 A a late prophase stage of the triploid wheat, where bivalents of both the closed and open type may be seen in addition to the univalents

In the metaphase the univalents may occasionally form a semi-plate (Fig 2 B), but they are almost invariably dispersed over the entire spindle (Fig 2 C) Bivalents, when present, lie in the normal position in the center of the spindle (Fig 2 D), and disjoin in the anaphase in the usual manner The univalents may move to the poles undivided and in irregular numbers depending on their location on the spindle (Fig 2 E) If, however, the movement to the poles is delayed and the anaphasic split occurs, it affects simultaneously all the univalents wherever they lie on the spindle A univalent lying at the equator will actually divide, adding one half to each pole A dividing univalent lying off the equator will add both its halves to the nearest pole (Fig 2 F)

The tetrads have a fairly regular appearance, but often micronuclei as well as miniature pollen grains are seen (Fig 5 M, N) Figure 5 L, from an ovule, shows the micropylar cell of the diad in the late prophase of a delayed division Approximately 10 chromosomes are observed, suggesting 11 chromosomes for its sister cell of the diad Unless all the rye chromosomes were represented in the inner cell, the chromosome complement was probably too unbalanced for proper functioning Be that as it may the two megaspores derived from the inner cell of the diad are in process of degeneration leading to sterility of the ovule

(c) *Aegilops-wheat Triploids*

TABLE 2 NUMBER OF BIVALENTS IN AEGILOPS-WHEAT TRIPLOIDS

Hybrid	Range	Mode	Author	Year
Ae ovata (14) x *T monococcum* (7)	0 5		Bleier	1927
Ae ovata x *T monococcum*	0-6		‘	1930
Ae ovata x T *monococcum* (Einkorn)	0 6	1 2 3	Aase	“
Ae ovata x *T villosum* (7)	0	0	Bleier	1927
Ae ventricosa (14) x *T villosum*	?-4	4	“	“
T turgidum var *buccale* (14) x *Ae speltoides* (7)	4-10	7	Jenkins	1928

Aegilops-wheat triploids may result from two forms of gamete combination, Aegilops 14 + wheat 7, or Aegilops 7 + wheat 14 Ac-

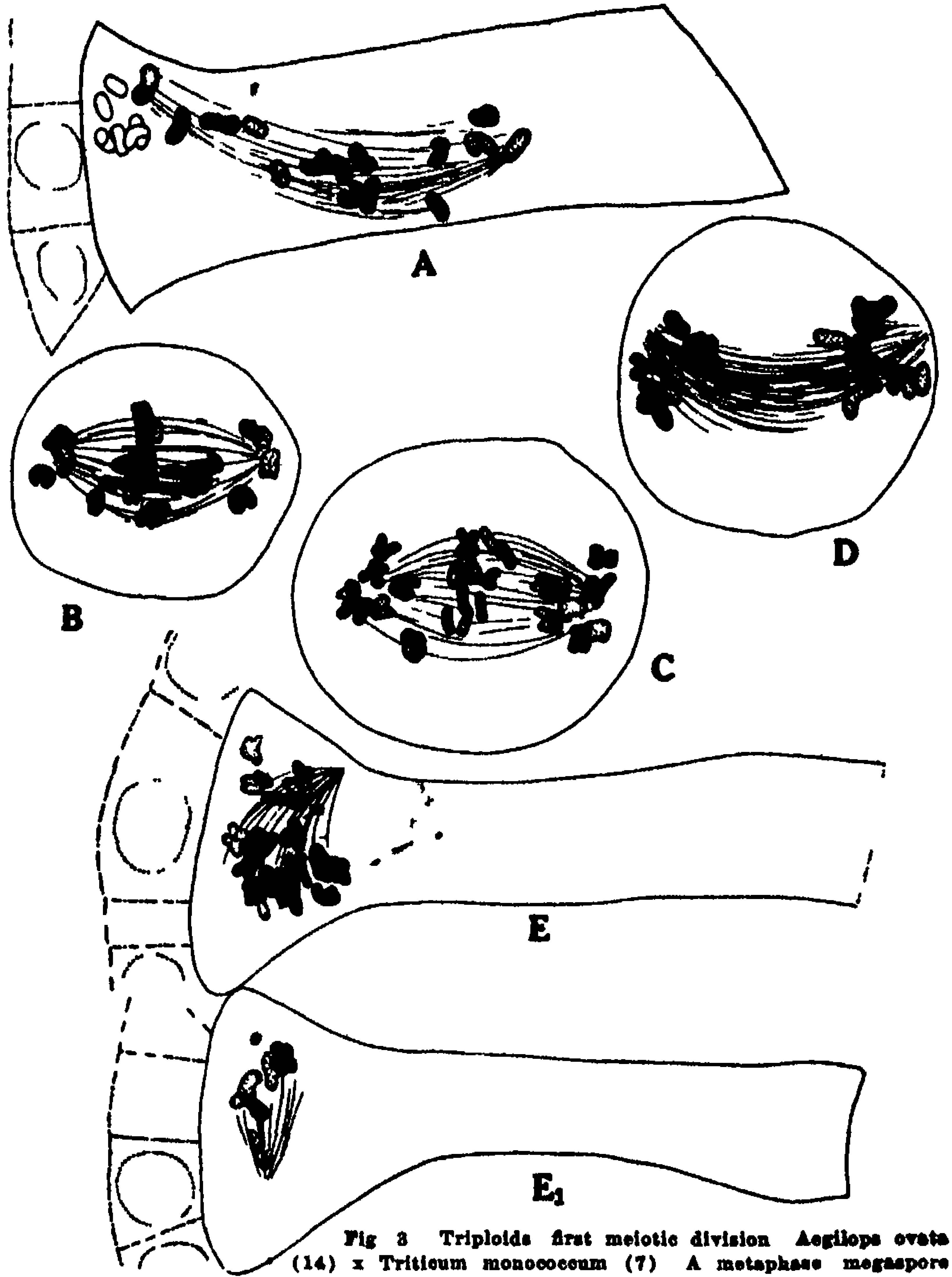


Fig 3 Triploids first meiotic division Aegilops ovata (14) x Triticum monococcum (7) A metaphase megaspore mother cell 21 univalents distributed over the elongated spindle (Unshaded chromosomes from other section) B 1 bivalent and 1 trivalent The equational split is appearing before the bivalent and trivalent have completed disjunction C anaphase The equational split having occurred the halves of univalents lying on the equatorial plate are beginning to migrate toward opposite poles D anaphase entire univalents migrating toward opposite poles the lone bivalent about disjoined

T compactum (21) haploid EE$_1$ megaspore mother cell (2 sections) The equational split has occurred in the 21 univalents and is suggestive of non reduction of univalents The short spindle is typical of this type of division X 1800 cording to table 2, the hybrids of the first combination form in general a smaller number of bivalents, but as the hybrids within this group vary in this respect with the species of Aegilops or wheat used, the significance is at present obscure

Bleier in comparing *Ae ventricosa* and *Ae ovata* when used as the respective Aegilops parents with *T villosum,* a wild grass from Italy, states "*Aegilops ventricosa* scheint demnach *Triticum villosum* naher zu stehen als *Aegilops ovata,* wenn man nicht Ausseneinflusse als Ursache fur die Paarung einiger Chromosomen annehmen will"

The Aegilops 14 + wheat 7 hybrids show decidedly weaker chromosome pairing than do the wheat triploids This is indicated both by the smaller number of pairs and also by the almost exclusively open type of pairs in the Aegilops-wheat triploids (Fig 4 and Table 10)

Ae ovata no doubt gives rise to a larger number of pairs in a cross with an einkorn wheat than in a cross with an emmer or a vulgare (Table 10) This is a puzzling fact and is at present difficult to explain *Ae ovata* may be a true tetraploid with the chromosome combination *d7* + *d7*, in which case it might be further suggested that autosyndesis could possibly occur more freely in combination with few than with many foreign chromosomes

One trivalent of the open or V type (Fig 4) occurs in about every tenth cell The bivalents and trivalents, when present extend through the equatorial plate, and the univalents are usually spread through the entire metaphase spindle in both the ovules (Fig 3 A) and the anthers (Fig 3 B) The bivalents and trivalents disjoin in normal manner In anaphase the univalents may go to the poles before splitting (Fig 3 D), or after (Fig 3 C) Rarely the bivalents and trivalents split equationally before disjunction is completed (Fig 3 B)

The comparatively large number of pairs, as reported by Jenkins for *T turgidum* x *Ae speltoides,* a hybrid of the reverse gamete combination, suggests possibly a closer relationship of this Aegilops to the emmer wheats The prevalence of the open type in the metaphase, as indicated by the illustrations, points to a relationship of somewhat ancient origin

(d) *Aegilops Triploid*

The only Aegilops triploid described cytologically is *Ae ovata* (14) x *Ae caudata* (7) Bleier (1927) observed bivalents varying in number from 7-10 on the equatorial plate, and as many as 7 scattered univalents When the components of the bivalents had reached the poles, the univalents collected at the equator and divided equationally, though in some cases univalents failed to divide Straying chromosomes were not observed The tetrads were normally 4-celled The hybrid was sterile

(e) *Haploid-wheat Triploid*

The haploid vulgare wheat, *T compactum* (Hybrid 128), formerly described by Gaines and Aase (1926), though not a hybrid of present origin may advantageously be compared with the triploid hybrids In the orientation of chromosomes and conjugation it resembles most closely the durum-rye cross, but shows still fewer conjugates

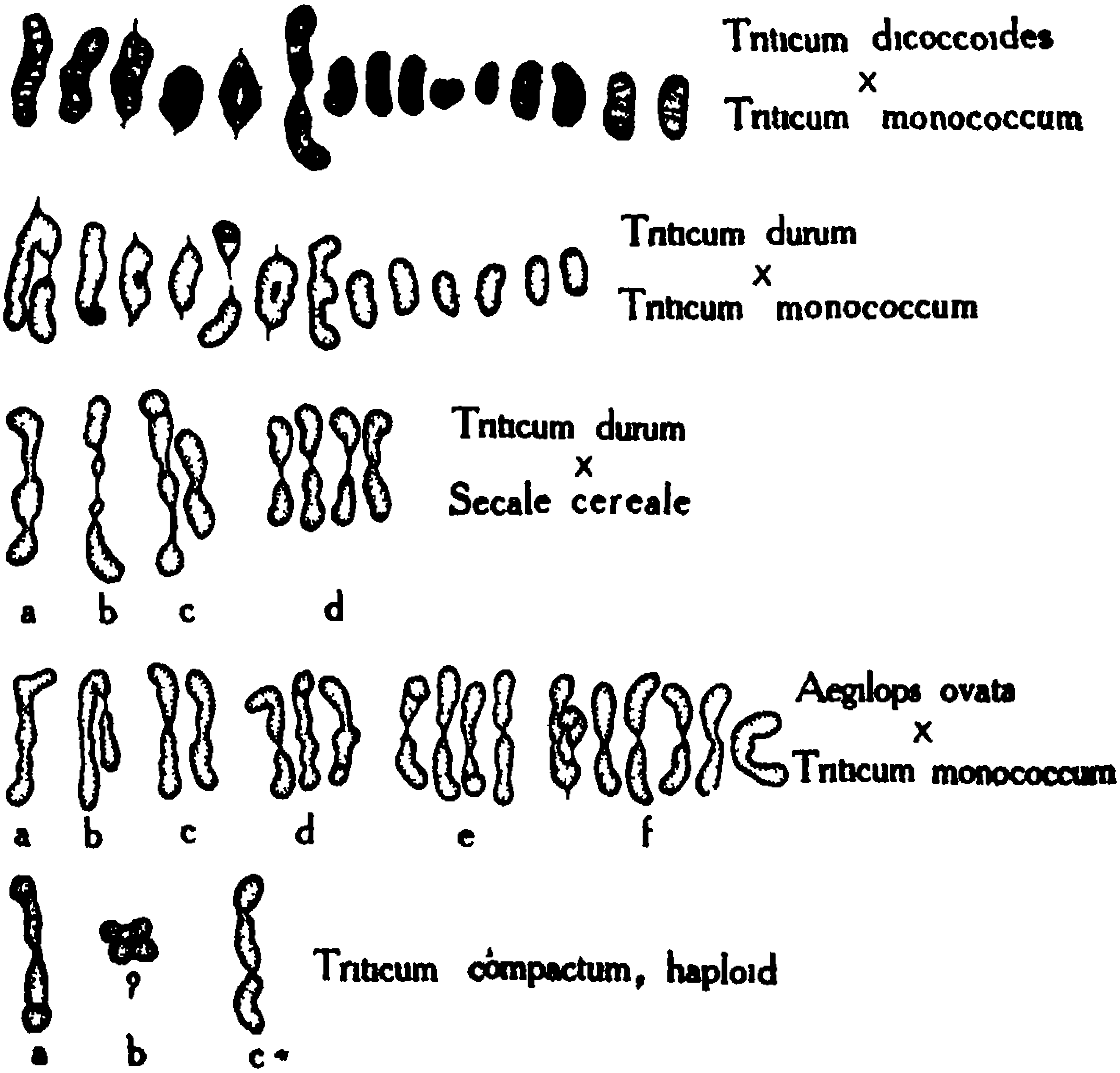


Fig 4 Triploids chromosome conjugation Entire chromosome complement of the microspore mother cells illustrated in the wheat hybrids Differential staining represented in first group (iron alum haematoxylin) a b c etc conjugates of respective spore mother cells X 1800

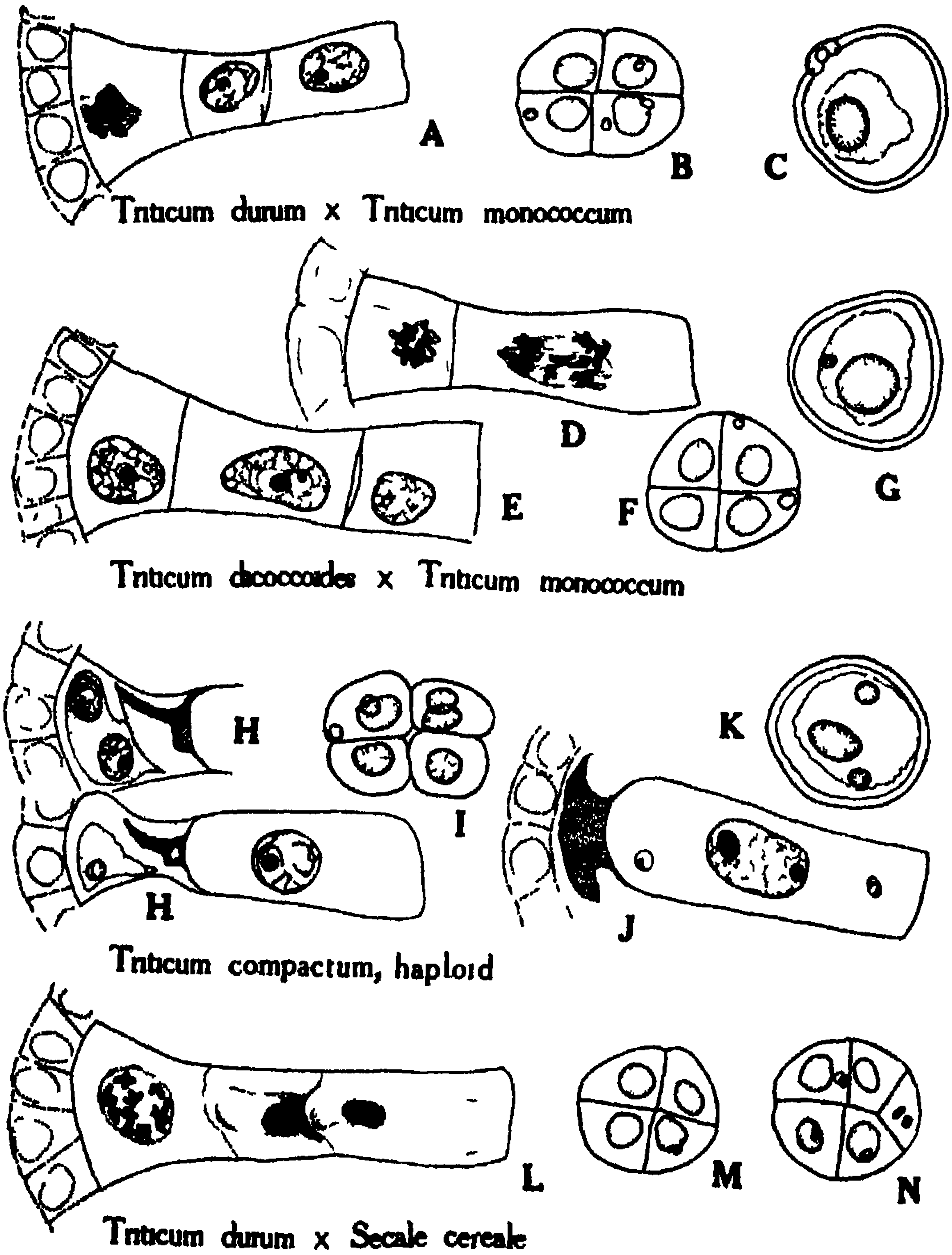

A
B
C
Triticum durum x Triticum monococcum
D
E
F
G
Triticum dicoccoides x Triticum monococcum
H
I
K
H
J
Triticum compactum, haploid
L
M
N
Triticum durum x Secale cereale

Fig 5 Triploids A N diads tetrads and pollen grains X 850

Tetrad and pollen formation presents the entire range of irregularity found in any hybrid. HH_1 I and K in figure 5 are conservative examples.

A few fertile seeds produced by the haploid developed into apparently normal diploid plants which exhibited meiotic divisions quite typical of the vulgare type. This indicates that at least some of the functioning megaspores of ovules contained the complete 21 chromosome complement of *T. compactum.* The slides on hand were reexamined for signs of a possible explanation. Only one or two suggestions were revealed. Figure 3 E and E_1, two sections of an ovule, show the univalents split as at the initiation of an equational division and though only the majority of the chromosomes are approximately at the equator they are all on a single spindle. Judging from the procedure in pollen mother cells of hybrids and the haploid only the chromosomes lying at the equator will actually divide. Only when all the univalents lie at the equator will all univalents divide equationally and each cell of the diad receive the entire complement of 21 chromosomes. Figure 5 D (Gaines and Aase, 1926) shows close approach to equational division of all the 21 chromosomes in a pollen mother cell.

Figure 5 J, a more advanced stage from an ovule appears like a diad, the micropylar cell of which is in a well advanced stage of degeneration. The nucleus is large as compared with the inner nucleus of figure 5 HH_1. Figure 5 J might possibly be a diad which has resulted from the equational division of all, or nearly all, of the 21 univalent chromosomes. The presence of the two micronuclei suggests straying chromosomes.

(f) *Aegilops-rye Triploid*

The cytology of Aegilops-rye has been described by Karpechenko and Sorokina (1929). Aegilops, the pistillate parent, was represented by two forms of *Ae. triuncialis* ssp. *typica* and by *Ae. triuncialis* ssp. *persica.* Rye, the pollen parent, was represented by *S. cereale* var. *afghanicum* and *S. cereale vulgare.* The reduction division in the pollen mother cells revealed usually 5, and less frequently 6 or 7, bivalents of the open type. The 7-11 univalents were scattered over the spindle.

The open type of pairing indicates feeble chromosome homology. As to the origin of the bivalents the investigators state "Whether in our hybrids the *Aegilops* chromosomes conjugate with the rye chromosomes or whether there takes place conjugation of *Aegilops* chromosomes between themselves (*autosyndesis*), cannot be answered as yet "

III TETRAPLOIDS

(a) *Wheat Tetraploids*

TABLE 3 NUMBER OF CONJUGATES IN WHEAT TETRAPLOIDS

Hybrid	Range	Mode	Author	Year
T durum (Kubanka) (14) x *T polonicum* (Polish) (14)	13 14	14	Aase	1930
T durum (Kubanka) x *T dicoccoides* (Wild Emmer) (14)	11 14	14	"	"
T monococcum (7) x *T spelta* (21)	0-5	3 4	Melburn & Thompson	1927
T spelta x *T aegilopoides* (7)	6-10*	7	Kihara & Nishiyama	1928
T vulgare (21) x *T monococcum* (7)	0 5	—	Bleier	1930

* Including trivalents

Tetraploids in wheat result from the gamete combination 14 + 14 or 21 + 7 The chromosome conjugation in the 14 or emmer combinations has been given in general for various crosses, and by different investigators, as 14 pairs The writer has found 14 pairs occurring rather uniformly in *T durum* x *T polonicum* and in *T durum* x *T diccoccoides* Unpaired chromosomes are sometimes observed, but as unpaired chromosomes may be found in apparently stable species and varieties, they may possibly not be due to the crossing The parents of the cross in question have not been critically examined for irregularities

T durum x *T dicoccoides* has approximately 2 open pairs per cell as against less than one per cell in *T durum* x *T polonicum* *T durum* x *T dicoccoides* shows one tetravalent in two out of five spore mother cells (Table 10) The tetravalents are usually either of the open U (Fig 6 B), or closed ring form (Fig 6 C), but occasionally assymmetrical as in figure 13 The frequent presence of one tetravalent suggests partial autosyndesis As no tetravalents have been found when *T durum* is crossed with *T polonicum* we might assume that *T dicoccoides* is the cause of the tetravalent in the cross Conjugation in the ovules assumes the same uniformity as in the anthers (Fig 6 A, D) The irregularities observed in meiosis of *T durum* x *T dicoccoides* are further borne out by the rather frequent occurrance of small nuclei in the tetrads and pollen grains (Fig 15 B, C, D)

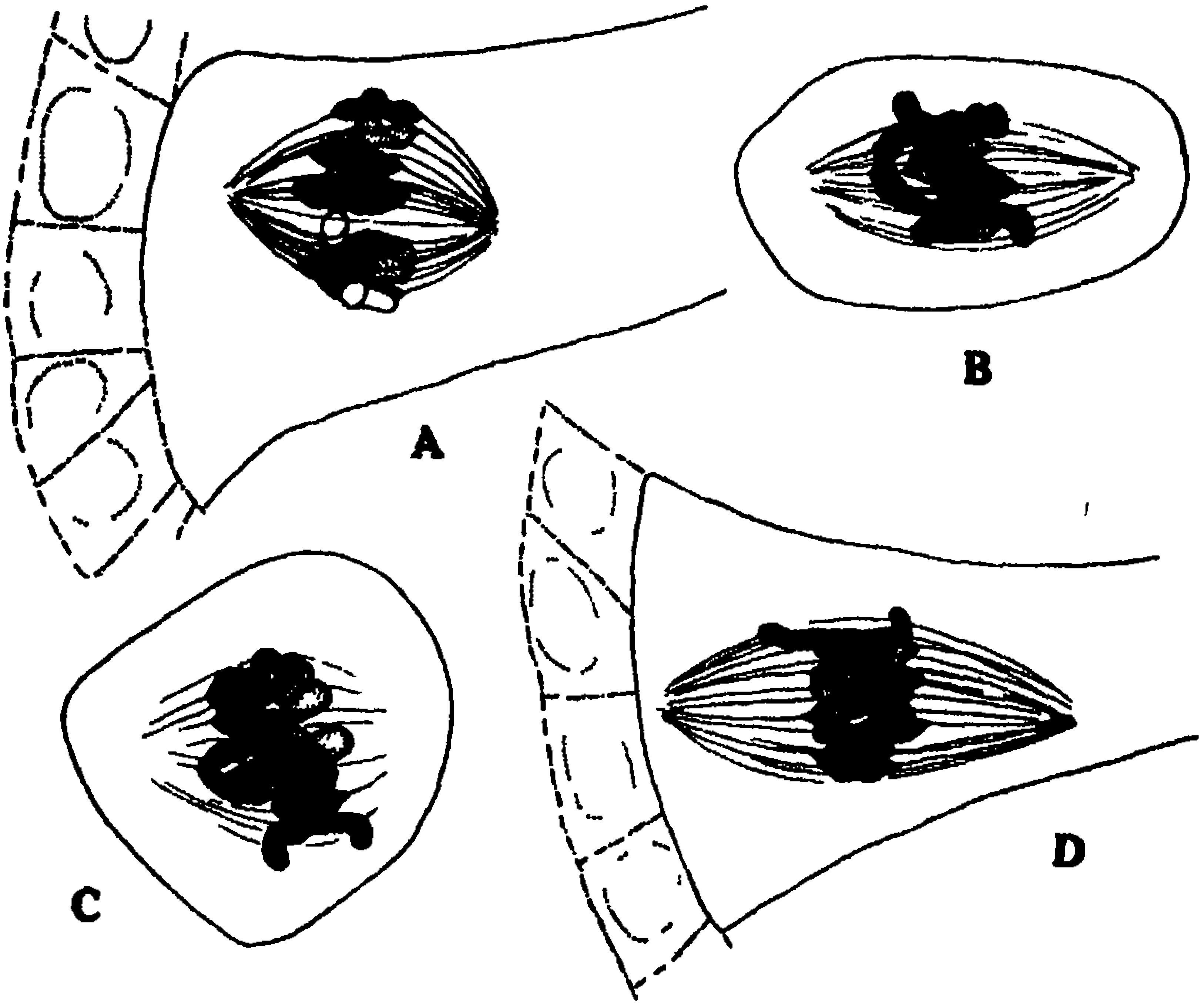


Fig 6 Wheat tetraploids first meiotic division Triticum durum (14) x T polonicum (14) A megaspore mother cell metaphase 2 unpaired chromosomes (unshaded from other section)

T durum x T dicoccoides (14) B metaphase showing a tetravalent of the open, or U form C (slightly diagonal) 11 closed and 1 open bivalents and 1 tetravalent of the closed or O type D metaphase megaspore mother cell 1 bivalent of the open type The spindle is comparatively short as is typical of the pure species and close crosses X 1800

The tetraploid wheat of the *7* + 21 gamete combination might be expected to simulate the triploid wheat as to number of bivalents This is in general found to be the case Two of the crosses of the *7* + 21 type reported cytologically involve *T spelta* as the 21-chromosome parent When *T monococcum* was used as the 7-chromosome parent 0-5 bivalents were observed by Melburn and Thompson, the mode lying around 3 to 4 The small number of bivalents together with the predominance of the open type of bivalents, as illustrated by these authors, would seem to indicate weaker chromosome homology than in triploid wheat hybrids

When *T aegilopoides* was used as the 7-chromosome parent the discrepancy apparently swung somewhat in the opposite direction, for Kihara and Nishiyama (1928) observed 6-10 conjugates, including sometimes 1 or 2 trivalents Seven bivalents were rather common These findings point to stronger pairing than is usually observed in the triploid crosses It may be that *T aegilopoides* stands closer than *T monococcum*, to *T spelta* A cytological study of a cross between *T aegilopoides* and *T monococcum* would be enlightening on this point

(b) *Wheat-rye Tetraploids*

TABLE 4 NUMBER OF BIVALENTS IN WHEAT-RYE TETRAPLOIDS

Hybrid	Range	Mode	Author	Year
T vulgare (21) x *S cereale* (7)	0 3	0	Kihara	1924
T vulgare x *S cereale*	0 2(?)	0	Zalensky & Doroshenko	1924-25
T vulgare var *albidum* x *S cereale*	0 3	0	Thompson	1926
T vulgare x *S cereale*	0 3	0	Bleier	1927
T vulgare x *S cereale*	0-4	0	‘	1930
T vulgare (Triplet) x *S cereale* (Rosen)	0 3	0	Aase	1930
T spelta (Alstroum) x *S cereale* (Rosen)	0-4	0	“	1930

The various cytological reports for the wheat-rye tetraploids are quite unanimous as to the small number of bivalents And as might be expected, the few bivalents that occur are prevailingly of the open type Of the two hybrids, studied by the writer, the *T vulgare*-rye only shows bivalents of the closed type (Fig 14 and Table 10), though the total number of bivalents is a little less than in the spelt-rye Traces of trivalents have been observed in both crosses (Table 10)

The univalents are as a rule dispersed over an elongated spindle, in both anthers (Fig 7 B, C and Fig 8 B, C) and ovules (Fig 8 A, E) The spindle finds more room in the ovules and usually stretches to the limit Pollen mother cells frequently present figures of curved spindles (Fig 7 B), giving the appearance of a spindle too big for the cell The curved spindles may occasionally be semi-tripolar, as if breaking at the bend (Fig 7 C) There appears to be a tendency in these disturbed hybrid mitoses toward overdevelopment in length of the spindles This tendency increases in general with the proportional increase of univalents over conjugates There are exceptions to this general statement when the greater majority of univalents are located at the equatorial plate positions, as in figure 7 A and figure 8 D, a rare occurrence in the wheat-rye hybrids

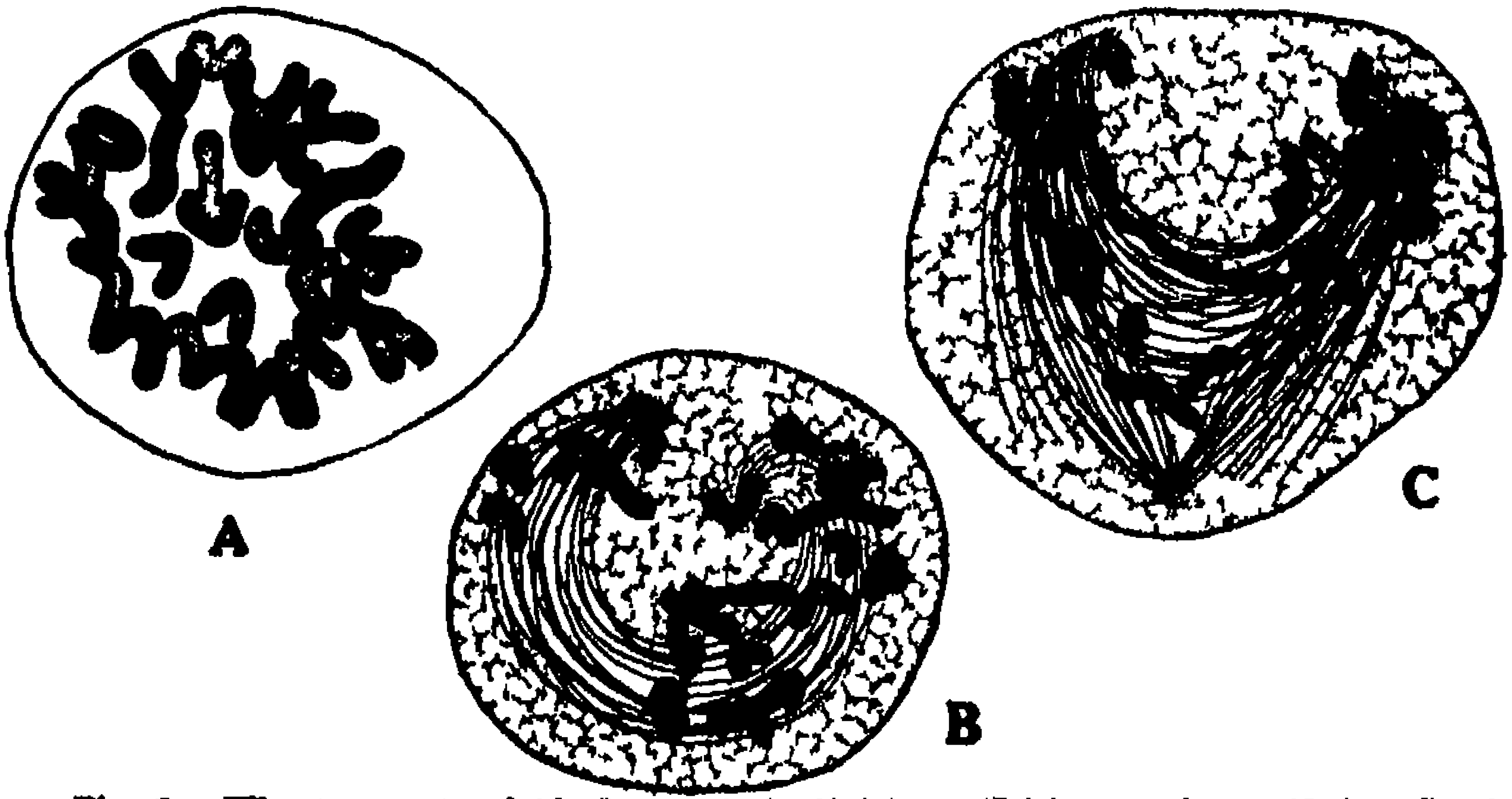


Fig 7 Wheat rye tetraploid first meiotic division *Triticum vulgare* (21) x *Secale cereale* (7) A metaphase polar view the rarely observed equatorial plate formation of the 28 univalents The 7 larger chromosomes are probably from rye B same stage as in A, but the typical arrangement of the 28 chromosomes over the spindle Curved spindles are frequently observed C combined curved and tripolar spindle One bivalent is in evidence X 1800

Aside from the more normal appearance of the spindle, the equatorial plate formation of the univalent chromosomes may carry a greater significance in that in its most complete form it makes possible the non-reduction of all the univalents, with the resultant complete chromosome complement in the two sister cells

The very irregular meiosis in the wheat-rye tetraploids gives rise to pollen tetrads which are quite fantastic as to number and size of cells and nuclei, and the size, shape, and nuclear state of resultant pollen grains (Fig 15 F-L)

(c) *Aegilops-wheat Tetraploids*

Three types of gamete combinations should be possible in producing tetraploid wheat-Aegilops hybrids wheat 14 + Aegilops 14, wheat 21 + Aegilops 7, and wheat 7 + Aegilops 21 Cytological descriptions are

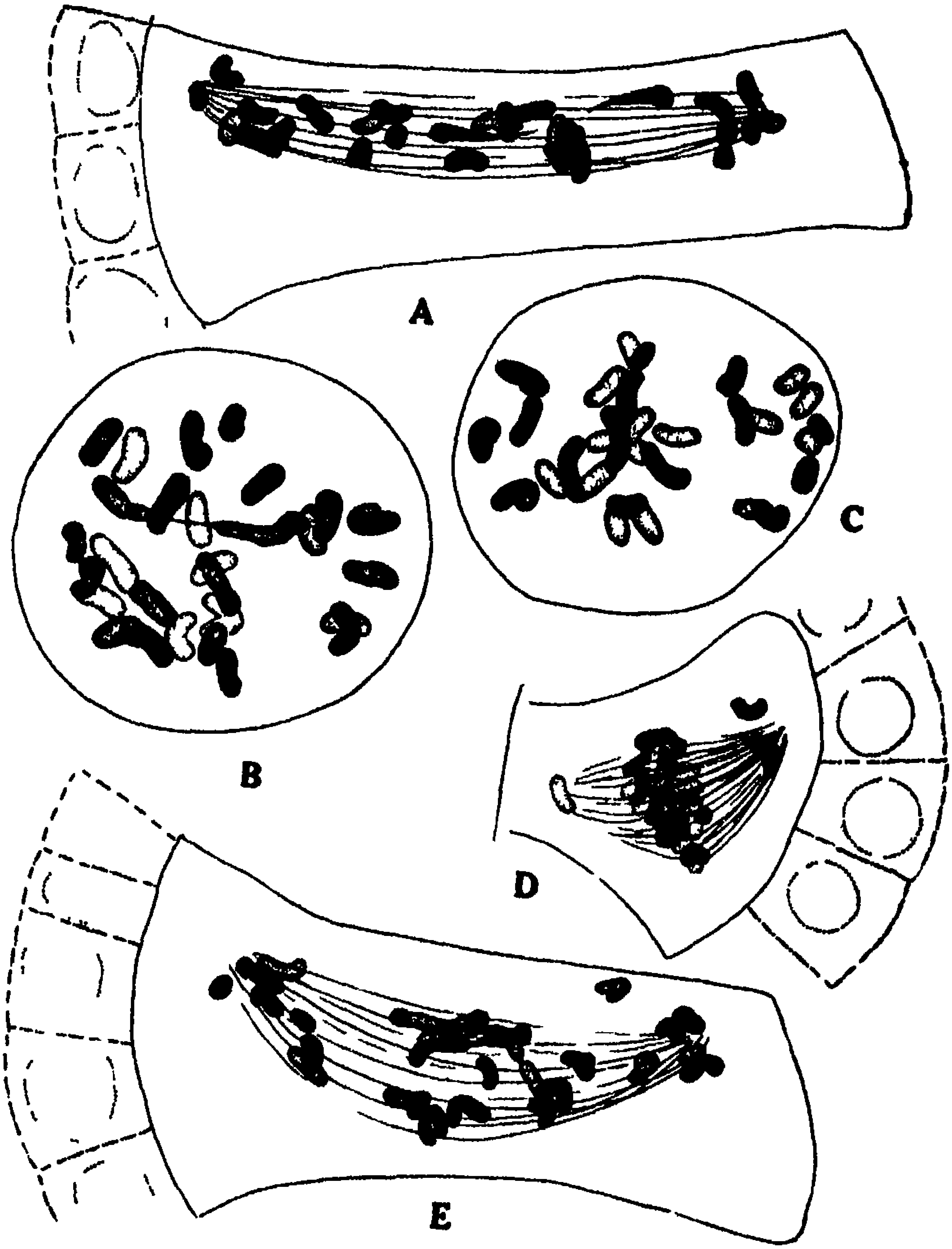


Fig 6 Wheat rye tetraploid first meiotic division Triticum spelta (21) x Secale cereale (7) A megaspore mother cell the lone bivalent in process of disjoining The 26 univalents are distributed through the elongated spindle typical of wide crosses with scanty conjugation B and C metaphase stage a side view (iron aceto carmine) D megaspore mother cell All but 3 of the 28 univalents are assembled on the equatorial plate the formation that results in division of a large number of univalents or in other words almost complete non reduction The short spindle is associated with the extensive equational division of univalents E megaspore mother cell 2 bivalents 1 trivalent, and 21 univalents X 1800

available of the 14 + 14 combination only *Ae cylindrica, Ae ovata,* or *Ae triuncialis* has been used as the Aegilops parent and in most cases as the pistillate parent At the State College of Washington it has been impossible to obtain the F_1 with wheat as the pistillate parent Seeds form as readily as in the reciprocal cross, but consistently fail to germinate The seed may be plump, but the embryo is either missing or defective Kihara has, however, obtained reciprocals when using *Ae ovata* as the pollen parent, showing that viable seed may be produced also on the wheat parent

TABLE 5 NUMBER OF CONJUGATES IN WHEAT-*AEGILOPS* TETRAPLOIDS

Hybrid	**Range**	**Mode**	**Author**	**Year**
Ae cylindrica x *T turgidum* (Alaska)	..	0	Gaines & Aase	1926
Ae cylindrica x *T durum*		0	Bleier	1927
Ae cylindrica x *T dicoccum* ..	0-4	0	Kagawa	1929
Ae cylindrica x *T turgidum* (Alaska)	0-4	0,1	Aase	1930
Ae cylindrica x *T durum* (Kubanka)	0 5	0 1	“	“
Ae ovata x *T dicoccum* var *Ajax* (Abyssinian Emmer)	?-7	..	Percival	1926
Ae ovata x *T dicoccum*	..	0	Sax	1927
Ae ovata x *T polonicum*	0 2	0	Kagawa	1929
T dicoccoides x *Ae ovata*..	0 6*	0 1 2 3	Kihara	‘
Ae ovata x *T dicoccoides*	0 3*	0 1	‘	“
T durum x *Ae ovata*	0-4*	0 1	‘	“
Ae ovata x *T durum*	1 7*	3 4 5	“	‘
Ae ovata x *T durum*	0-3		Bleier	1930
T dicoccoides x *Ae ovata* ..	0	0	“	“
Ae ovata x *T durum* (Kubanka)	0-4	0 1	Aase	“
Ae triuncialis x *T dicoccoides*	0 7*	2,3 4	Kihara	1929
Ae triuncialis x *T durum* ..	0-8*	4 5 6	“	“
Ae truncialis x *T polonicum*	3 8*	5,6	“	“
Ae triuncialis x *T dicoccum*	1 7*	4,5	“	“

* Including trivalents

The summary of the cytological reports (Table 5) shows clearly that these crosses tend to fluctuate somewhat in respect to chromosome conjugation which is shown to be generally weak in all the forms The bivalents are evidently prevailingly of the open type, as shown by the available illustrations and descriptions regarding this point The writer found an occasional closed bivalent (Fig 14) The conjugates in the various mother cells are suggestive of those in the wheat-rye crosses

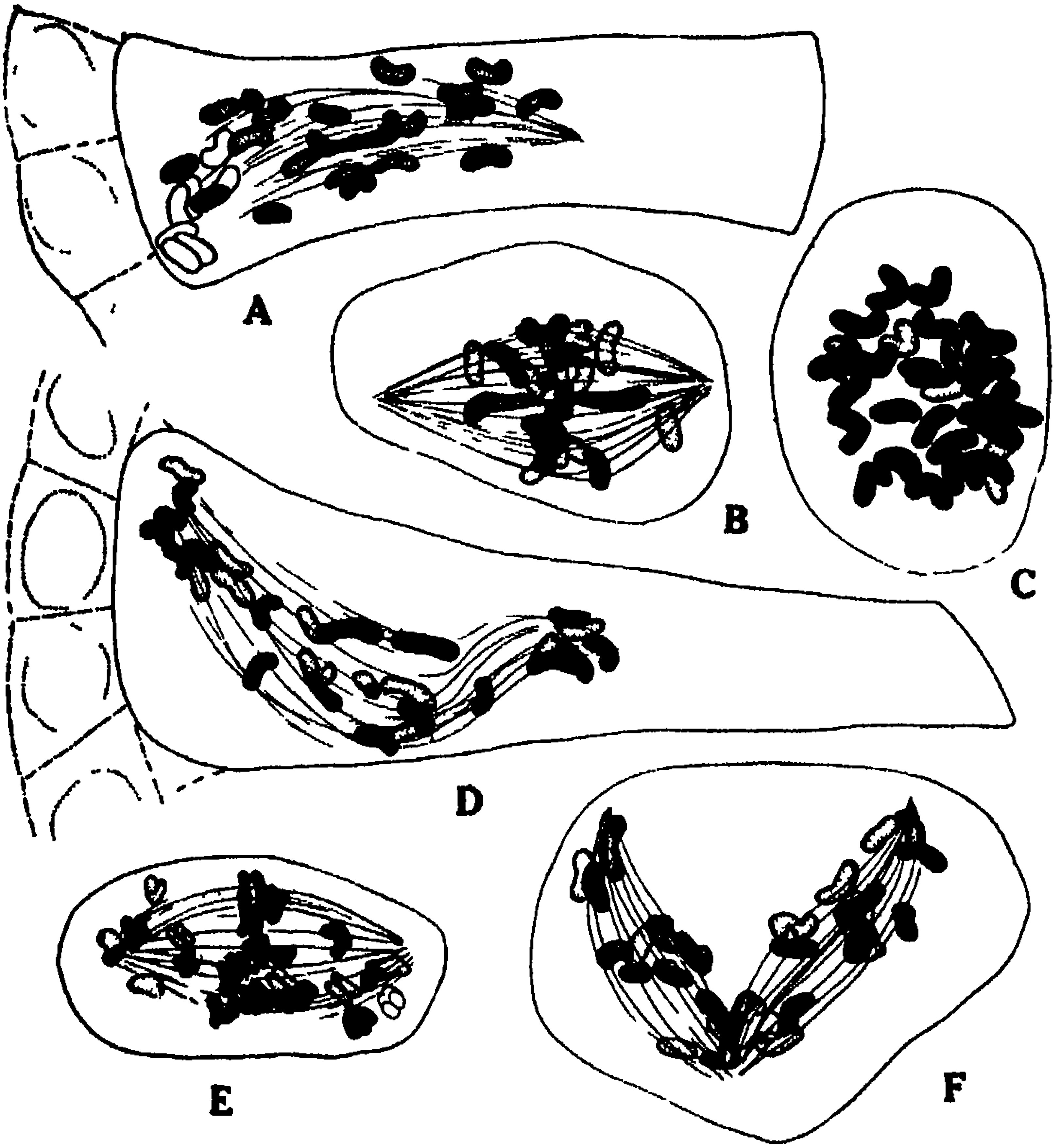


Fig 9 Aegilops wheat tetraploid first meiotic division Aegilops ovata (14) x Triticum durum (14) A megaspore mother cell 3 open bivalents and 22 univalents (Unshaded chromosomes from the lower section) B 1 bivalent and 26 univalents somewhat clustered toward the center of the spindle C polar view showing the rather infrequent formation of a polar plate D megaspore mother cell No typical bivalents in evidence The univalents are scattered in usual manner throughout the elongated spindle E anaphase All univalents have split and some lying near the center of the spindle are beginnig to separate into halves F semi divided spindle each wing carrying approximately 14 chromosomes X 1800

(Fig 14) One, and even two, trisomes have sometimes been found in *Ae cylindrica* x *T durum* (Fig 11 A, C, and Fig 14), and less frequently in the other two hybrids

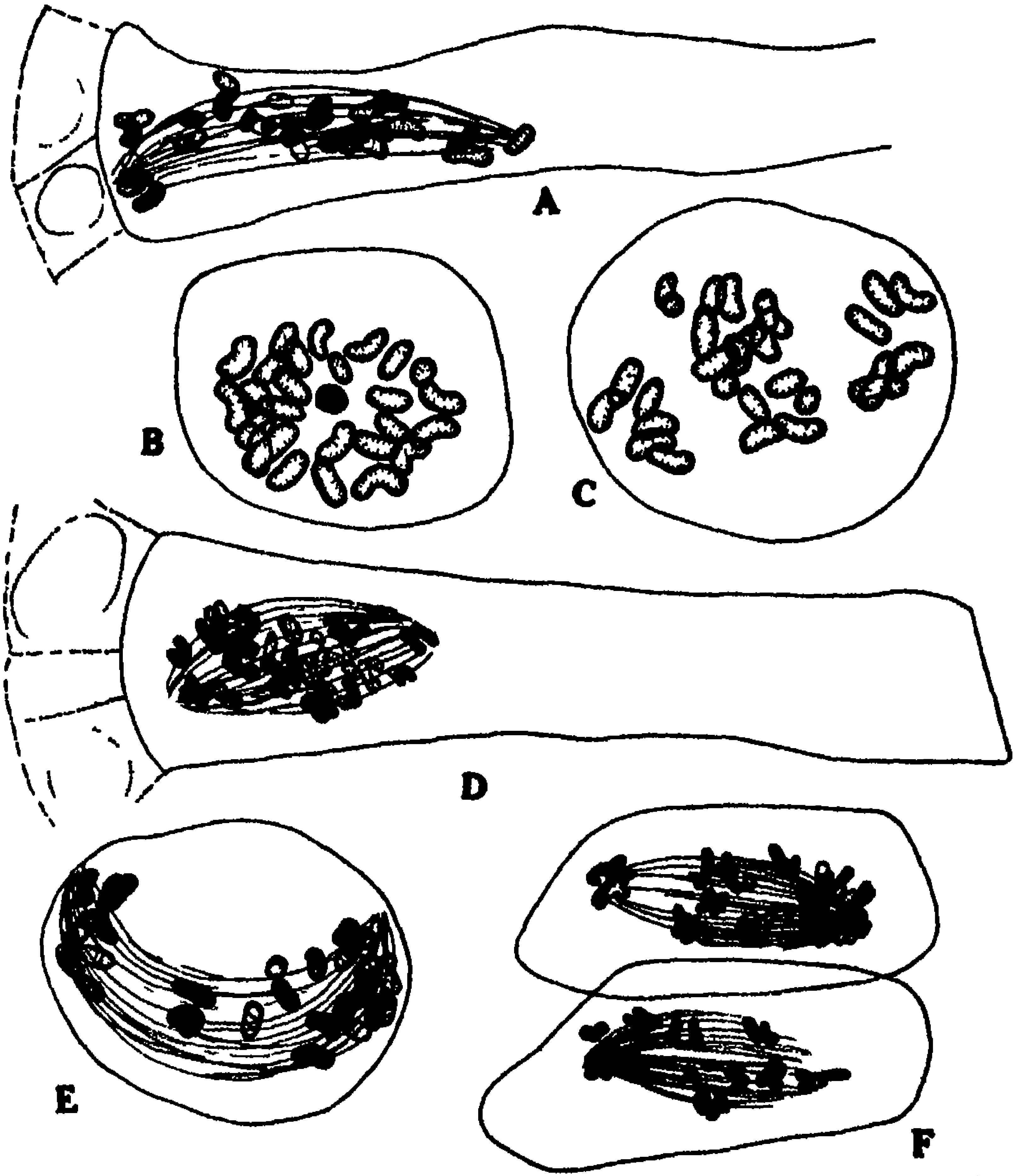


Fig 10 Aegilops wheat tetraploid first meiotic division Aegilops cylindrica (14) x Triticum turgidum (14) A megaspore mother cell 2 bivalents 1 trivalent and 21 univalents (4 unshaded chromosomes from lower section) B polar view of the rarely occuring polar plate 1 bivalent and 26 univalents C 28 univalents (iron aceto carmine) D megaspore mother cell incomplete non reduction of univalents The short spindle is typical of this type of division E 28 univalents Curved spindle frequently found Differential staining in chromosomes is indicated (iron alum haematoxylin) F upper and lower sections of a pollen mother cell Semi non reduction of univalents X 1800

As in many wide crosses the numerous unpaired chromosomes are scattered through the spindle, which in the ovules especially, is considerably elongated (Fig 9 A, D, Fig 10 A, C, E, and Fig 11 A, C, D) The length of the spindle may be further increased in pollen mother cells by curved spindles (Fig 10 E) Divided spindles are rarely found, and these may possess one pole in common (Fig 9 F, and Fig 11 E) or be independent spindles (Fig 11 B) It is an interesting coincidence, at least, that all dichotomously divided spindles observed carry on each wing or division the approximate number of chromosomes contributed by the respective parent

Disjunction of any bivalents or trivalents present takes place usually in the normal manner The behavior of the univalents, according to the writer's interpretation, depends largely on their location on the spindle at the time of the equational split (Fig 9 E, and Fig 10 F) The rather infrequent and as a rule somewhat imperfect, plate formation of the univalents (Fig 9 B, C, and Fig 10 B) leads to their more extensive equational division (Fig 10 D, and Fig 11 F F$_1$) Or, in other words, the plate formation tends towards non reduction of univalents Figure 11 G is of interest because it again suggests either a delayed disjunction of bivalents or a premature equational split of all the chromosomes

The tetrads and pollen grains show all degrees of irregularity (Fig 15 M-Q, and Fig 16 A-O) A pollen grain usually varies in size in direct proportion to the amount of nuclear material it contains The miniature pollen grains are usually perfect as to cell wall and pore Some of the larger pollen grains may contain more than one pore (Fig 16 G) Ovule tetrads of the type illustrated in figure 16 A and J no doubt lead to abortive ovules Figure 16 C illustrates an ovule diad, apparently, whose inner cell is enlarging preparatory to the formation of an embryo sac It is probable that this diad is the result of a division as represented in figures 10 D and 11 I F$_1$ The large amount of nuclear material and the three nucleoli indicate a large chromosome complement It is probably this type of ovule that contributes to seed development

Chromosome conjugation in these Aegilops-wheat tetraploids is erratic as evidenced by the varying reports Kihara found that the degree of conjugation may vary considerably within a cross He carried on a number of experiments to find the effect of reciprocal crossing, time of pickling, etc, and summarizes his conclusions as fol-

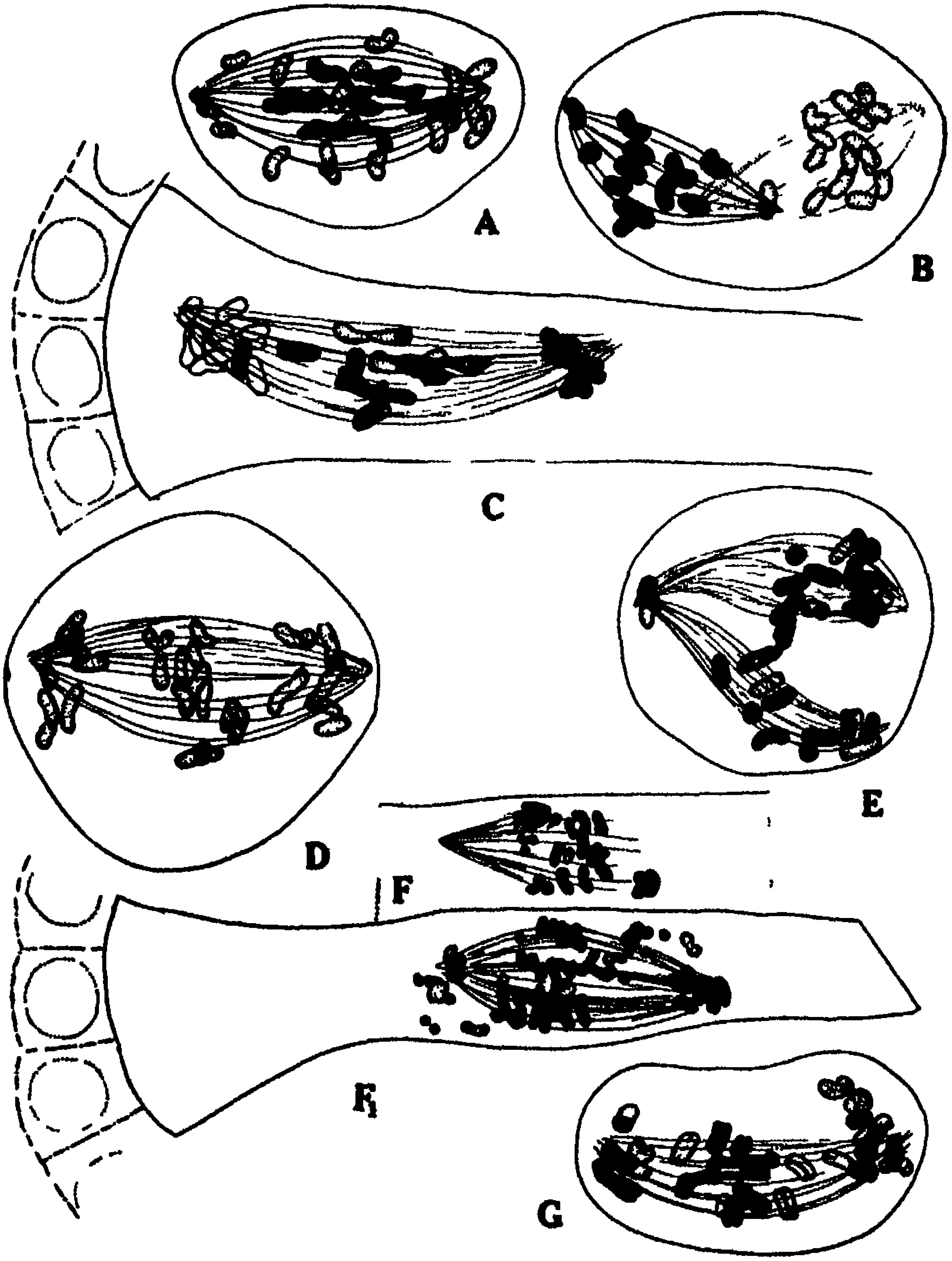


Fig 11 Aegilops wheat tetraploid first meiotic division Aegilops cylindrica (14) x Triticum durum (14) A 2 bivalents 2 trivalents and 18 univalents B two distinct spindles the upper bearing 13 univalent chromosomes the lower 15 C megaspore mother cell, 3 bivalents 1 trivalent and 19 univalents (Unshaded chromosomes from lower section) D 28 univalents distributed over spindle in usual manner E semi divided spindle one wing carrying 12 chromosomes the other 14 1 bivalent bridging the two wings FF_1 two sections of a megaspore mother cell incomplete non reduction of univalents Compare length of spindle with C G equational split appearing in all the chromosomes before the disjunction of the two bivalents X 1800

lows "   the divergence of variations of the same or similar crosses may be due chiefly to external conditions, but it is not certain what condition or conditions may be effective as the source of variations We can only suggest that temperature might have such influence "

The writer finds variations quite evident in the material studied More counts were made (one block of which is summarized in table 10) in these crosses, than in any of the other crosses, in an effort to obtain a fair average Anthers from one plant, as well as anthers from different plants, vary as to the extent of conjugation Counting is slightly more difficult when the conjugates are few and of the loose end-to-end type, in that the disjunction must be noted more carefully

(d) *Aegilops Tetraploids*

TABLE 6 NUMBER OF CONJUGATES IN AEGILOPS TETRAPLOIDS

Hybrid	Bivalents	Trivalents	Author	Year
Ae ovata x *Ae ventricosa*	5 10*	?-4	Kihara	1929
Ae ventricosa x *Ae ovata*	3 8*	?-3	"	"
Ae ovata x *Ae triuncialis*	5 11*	?-6	"	"
Ae cylindrica x *Ae ovata*	3 8	0-4	Aase	1930

* Including trivalents

Two types of gamete combinations may result in an Aegilops tetraploid, 7 + 21 or 14 + 14 Cytological data are available on the last only (Table 6)

The writer has examined cytologically *Ae cylindrica* x *Ae ovata* and confirms most heartily Kihara's statement that "Chromosomes of P M C of the species hybrids are very difficult to study" It is necessary to make complete drawings of the chromosome complement of the cell to determine the various combinations It is then sometimes impossible to interpret the combinations Besides univalents, bivalents, trivalents, and tetrasomes there are often larger groups (Fig 13 a, b, c) Sometimes these groups may be interpreted as pentasomes or hexasomes but other times the combinations are so exotic as to baffle any interpretation The meiotic picture is quite different from that of the 14 + 14 wheat tetraploids (Fig 13 and Table 10) The bivalents are nearly three to one of the open type The trivalents are most frequently of the V or Y types (Fig 12 A, B, C, and Fig 13)

The tetrasomes are not of the U or O type found in the wheat tetraploids The most prevalent type probably is a modification of the U type, two pairs being united in reverse position to form an N Univalents vary in number from 3-10 with an average approaching close to 7 The conjugates, of whatever combination, lie near the center of the spindle while the univalents may be widely distributed (Fig 12 A, B, C) The spindle of the ovule does not present that elongated appearance observed in the Aegilops-wheat tetraploids, and found so typical of very weak conjugation but has more the proportions of spindles

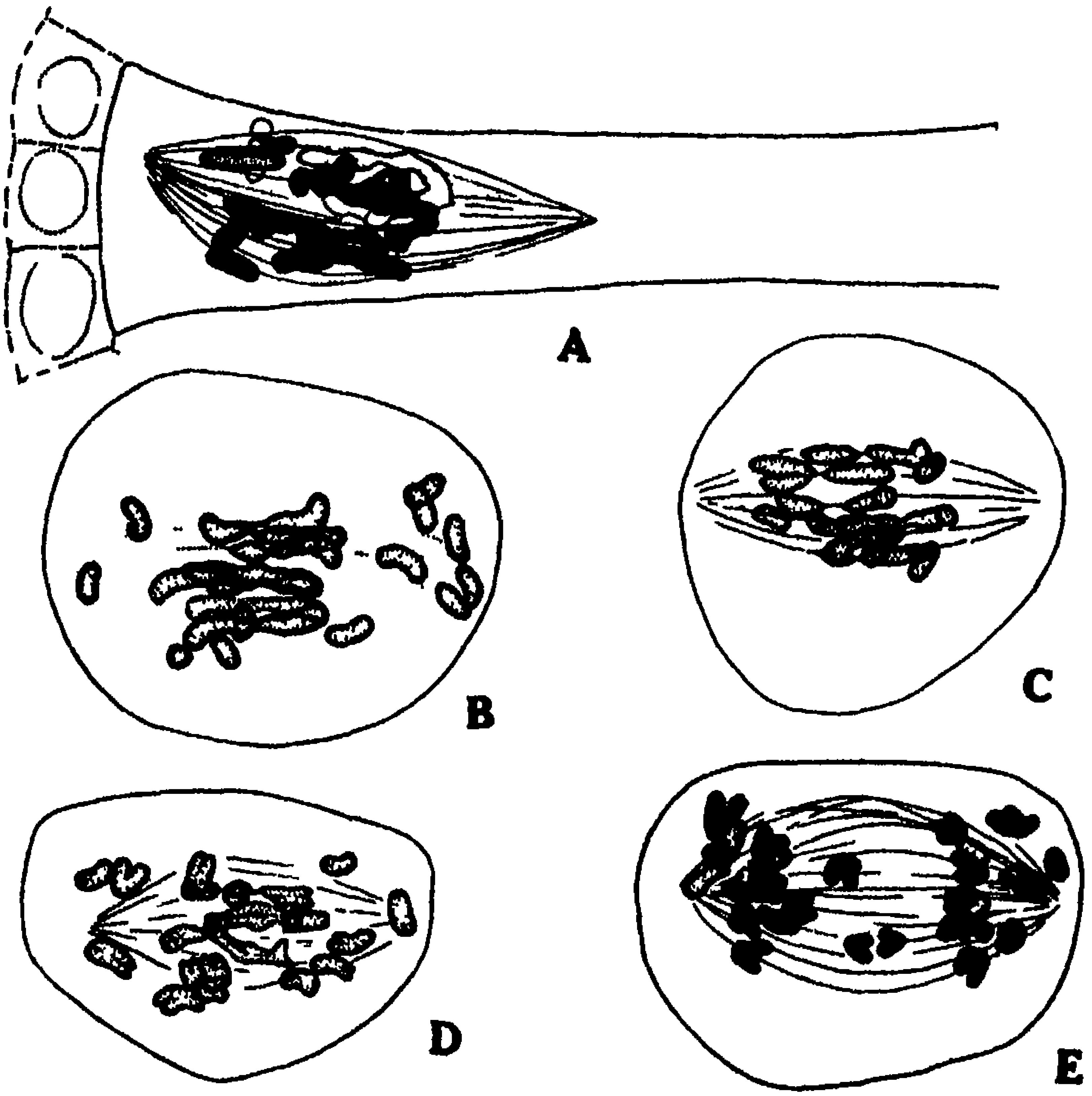


Fig 12 Aegilops tetraploid first meiotic division Aegilops ovata (14) x Ae cylindrica (14) A megaspore mother cell showing univalents bivalents 3 trivalents and 1 tetravalent (Unshaded chromosomes from lower section) B 8 open bivalents and 3 trivalents C 8 open bivalents and 2 trivalents about to disjoin (One of two sections) D equational split appearing in all chromosomes before the disjunction of bivalents E anaphase All univalents have split and one lying in the center of the spindle is dividing X 1800

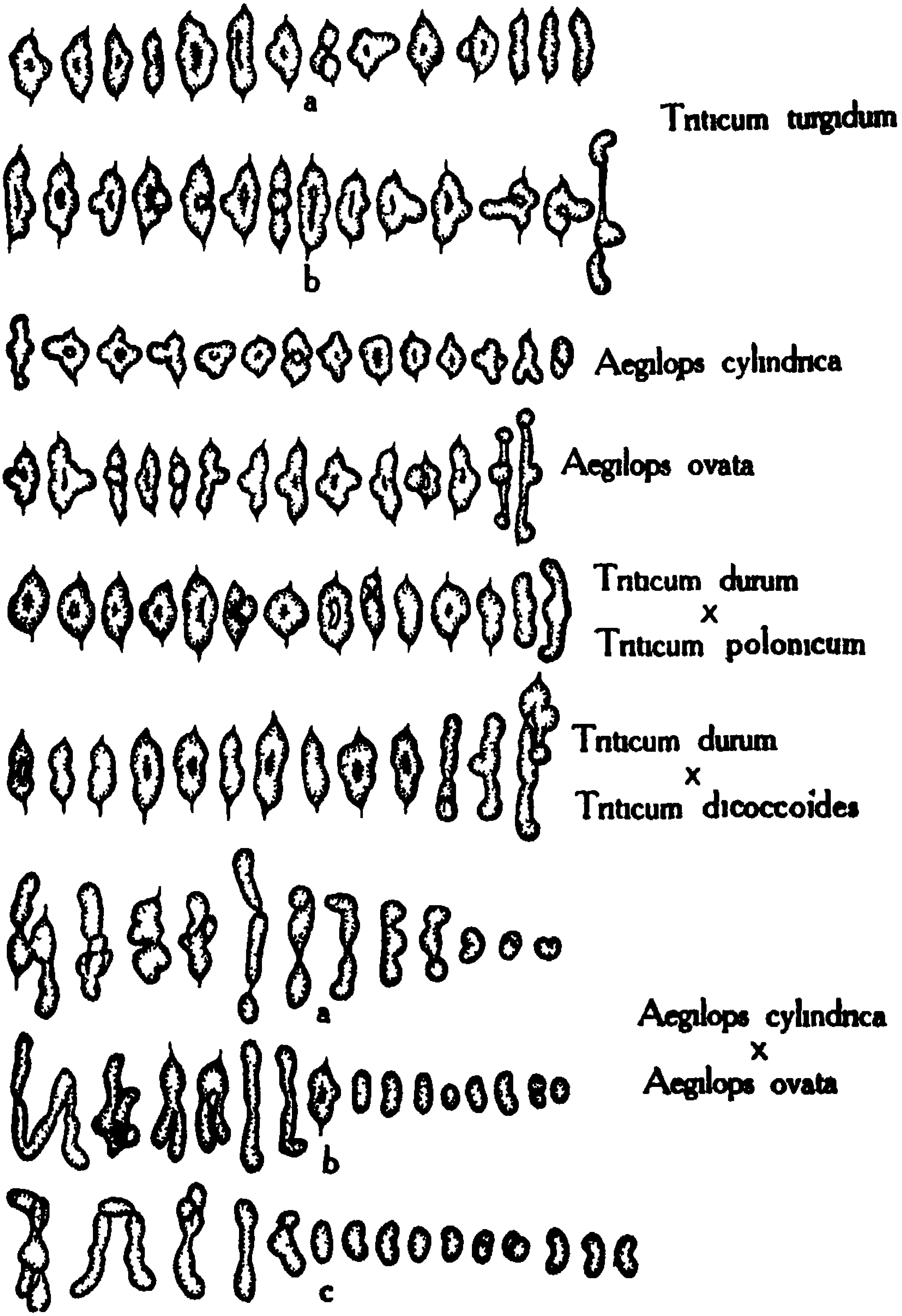


Fig 13 Tetraploids chromosome conjugation a b c chromosome complements of respective spore mother cells X 1800

observed in the ovules of the 14 + 14 wheat tetraploids The disjunction proceeds remarkably orderly (Fig 12 C, E), giving very nearly equal numbers of chromosomes to each pole Very few of the univalents have been observed to divide longitudinally in the first division, possibly because so few as a rule lie at the equator of the spindle

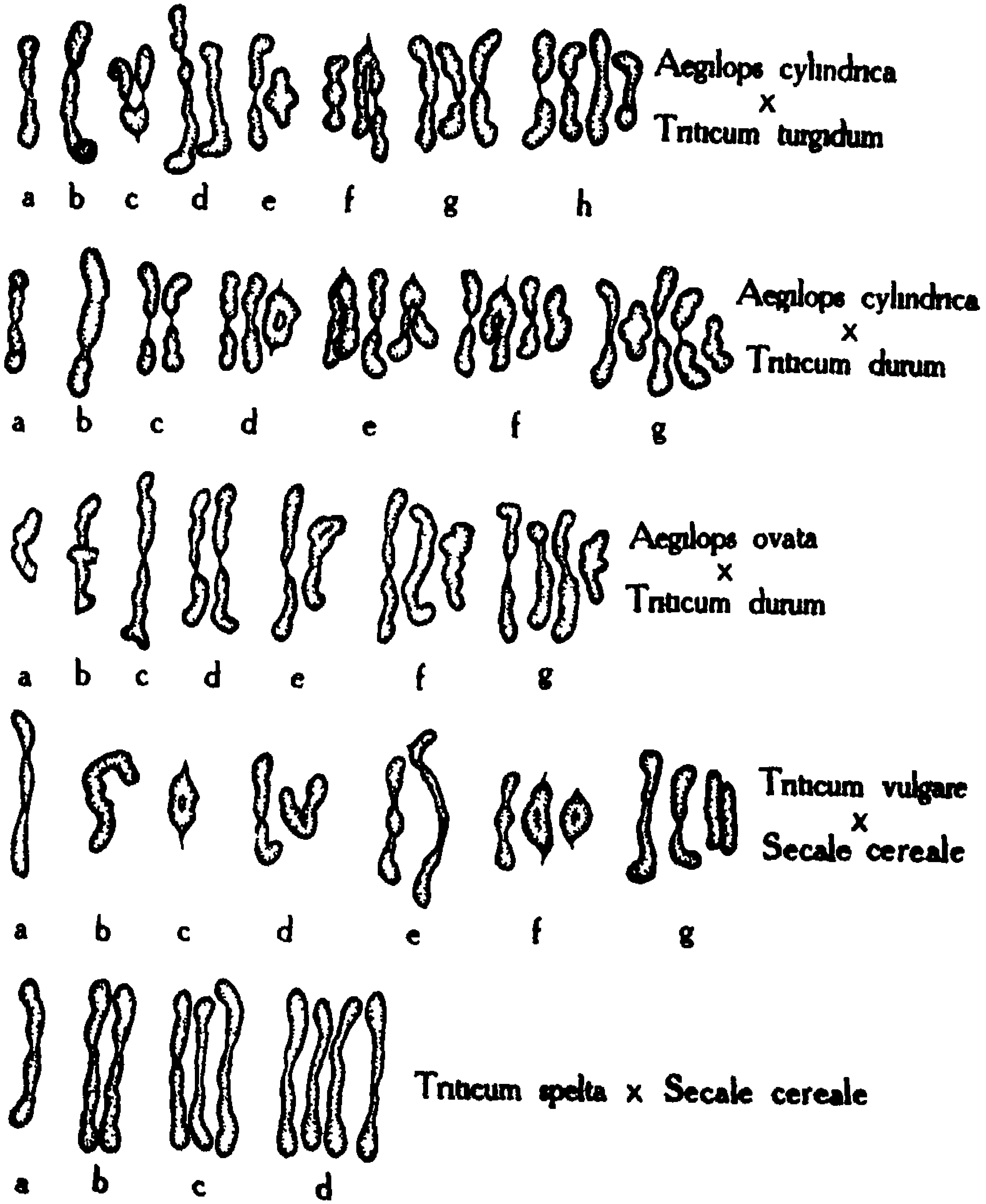
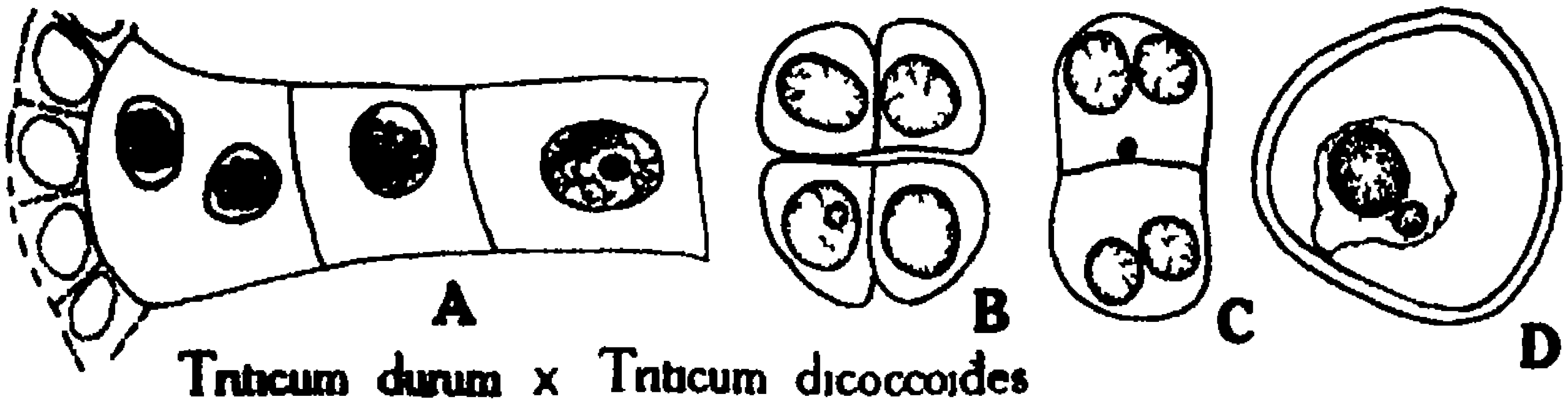
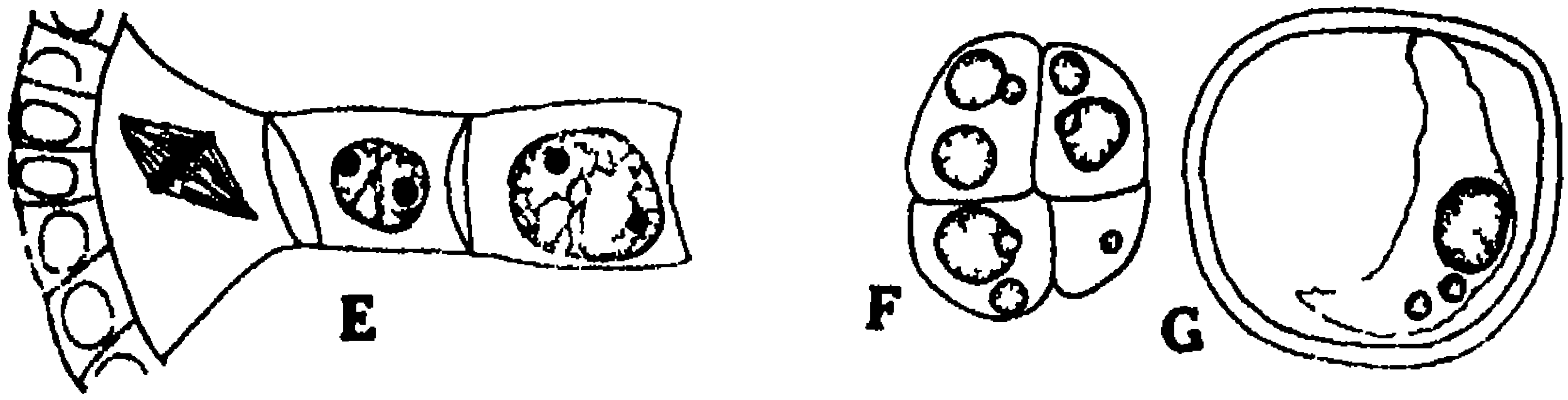


Fig 14 Tetraploids Chromosome conjugation a, b c etc conjugates of the respective spore mother cells X 1800

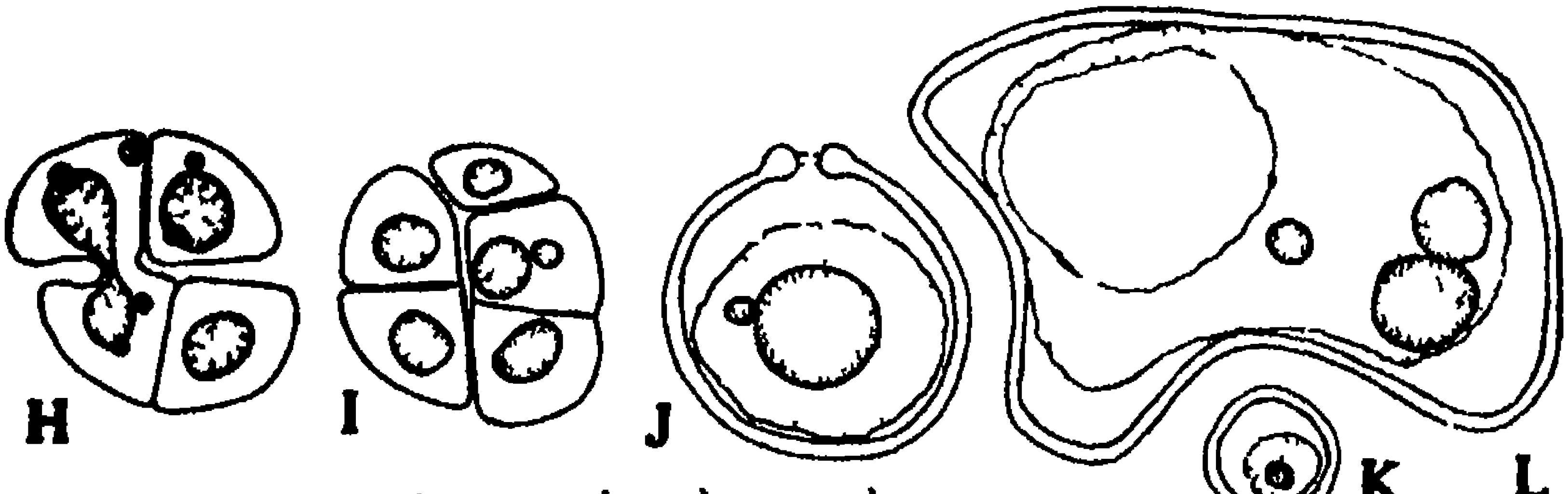


Triticum durum x Triticum dicoccoides

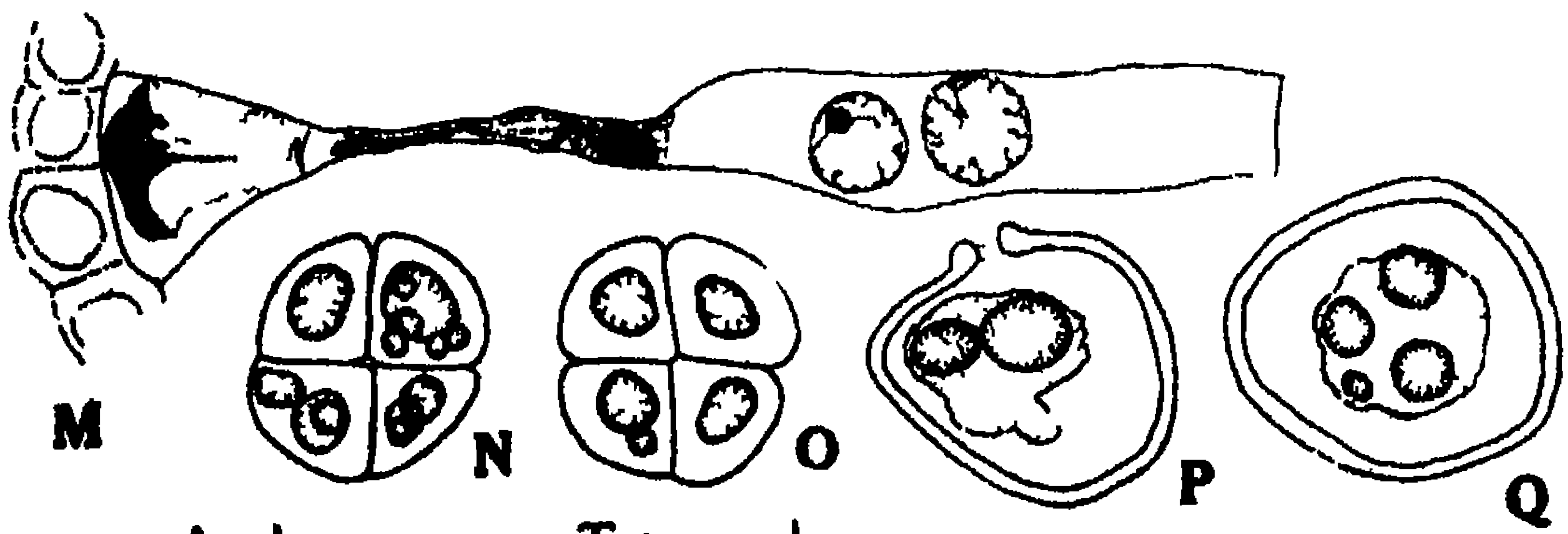


T. durum x T. polonicum

Triticum spelta x Secale cereale



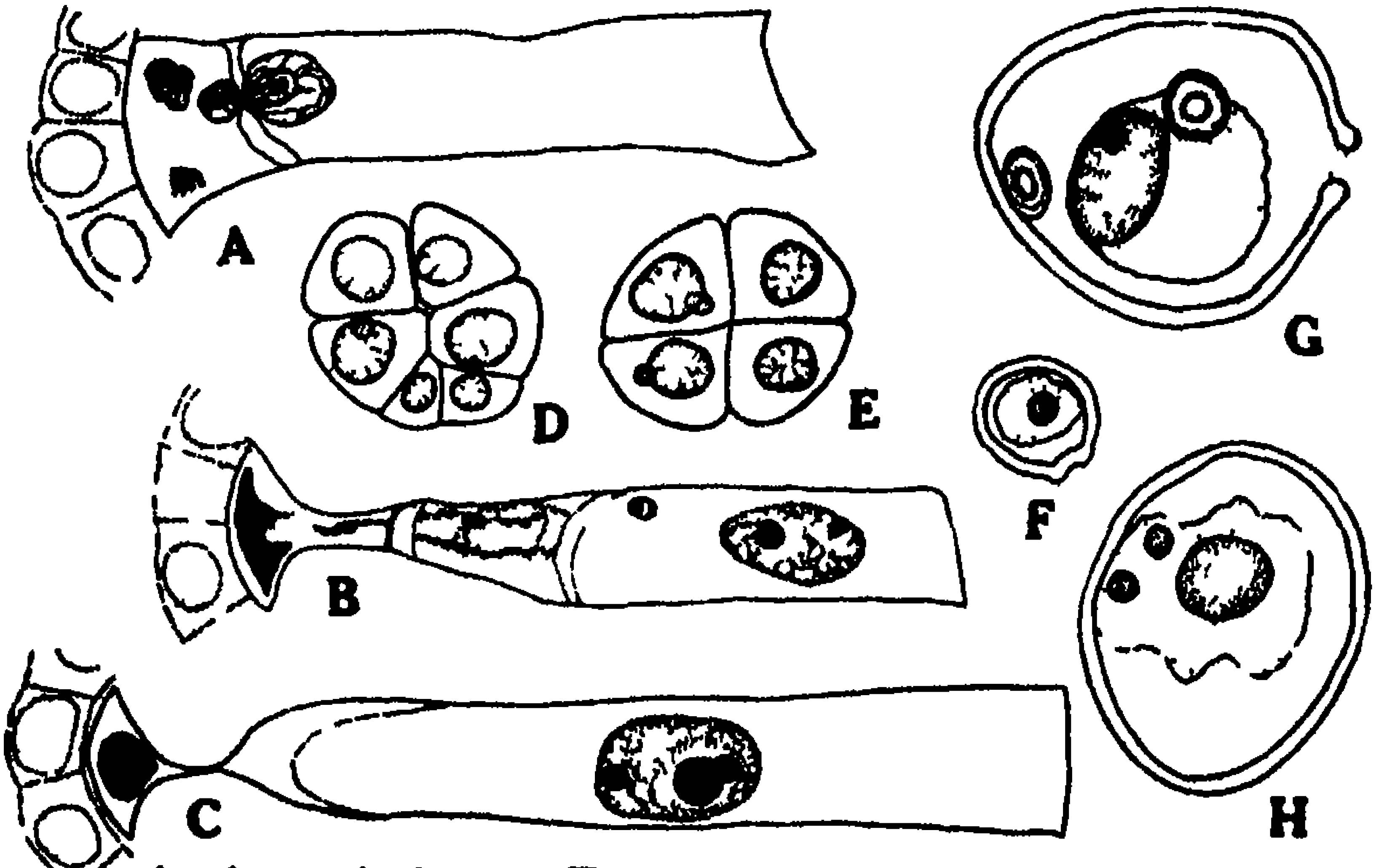
Triticum vulgare x Secale cereale



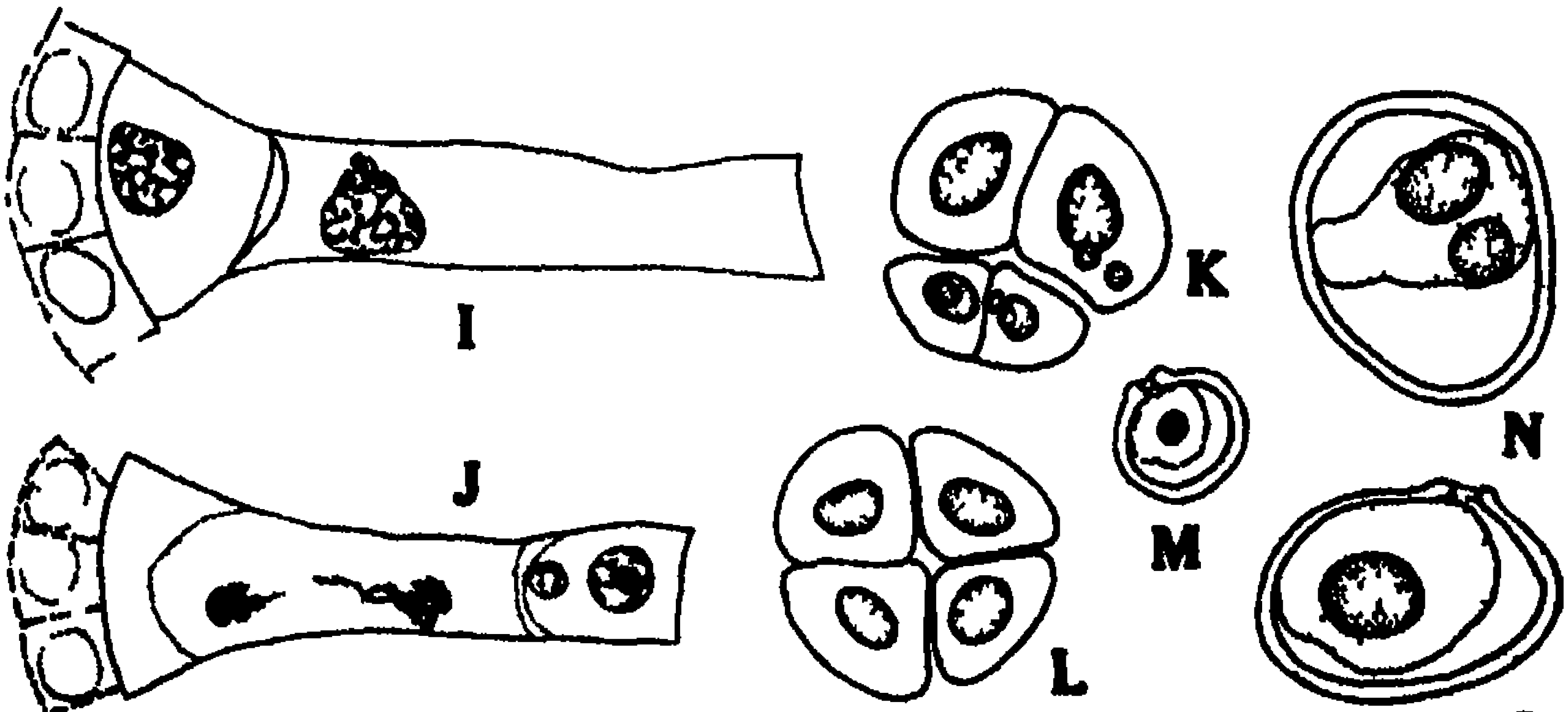
Aegilops ovata x Triticum durum

Fig 15 Tetraploids A Q diads tetrads and pollen grains X 650

Tetrads in both ovule and anther as well as pollen grains are rather regular in appearance (Fig 17 G-I) Small supernumerary nuclei are, however, frequently found, but micronuclei have occasionally been found also in pollen grains of *Ae ovata* (Fig 17 E, F) The F_1 was nevertheless completely sterile, indicating probably an unbalanced reduction of the chromosome complement The Aegilops triploid, described by Bleier, also was sterile Kihara states concerning the

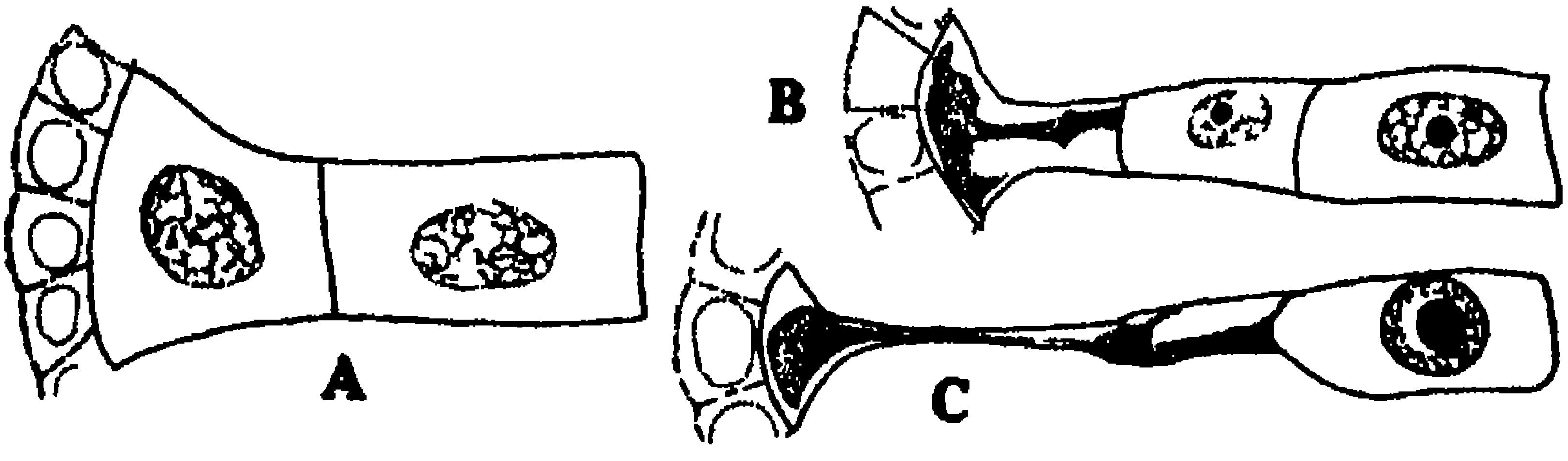


Aegilops cylindrica x Triticum turgidum

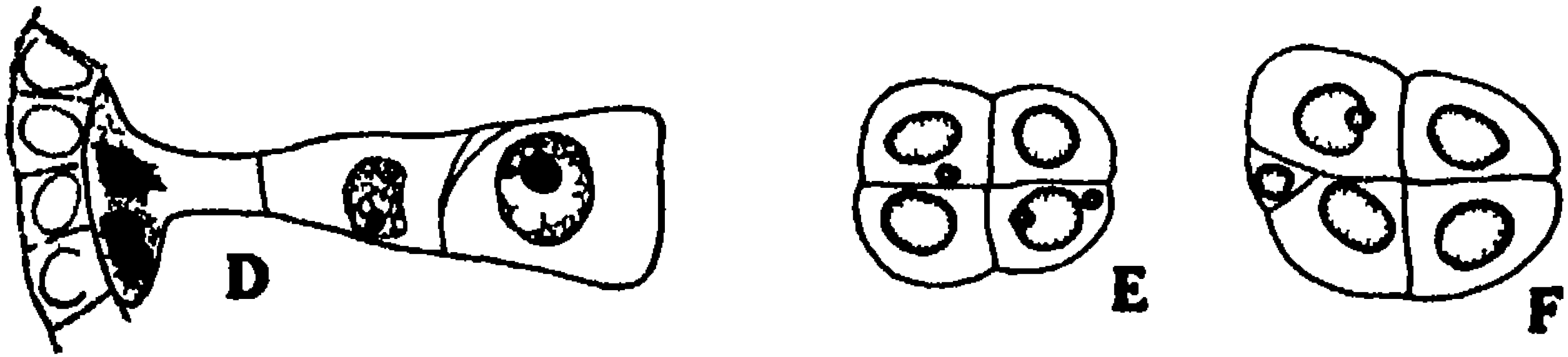


Aegilops cylindrica x Triticum durum

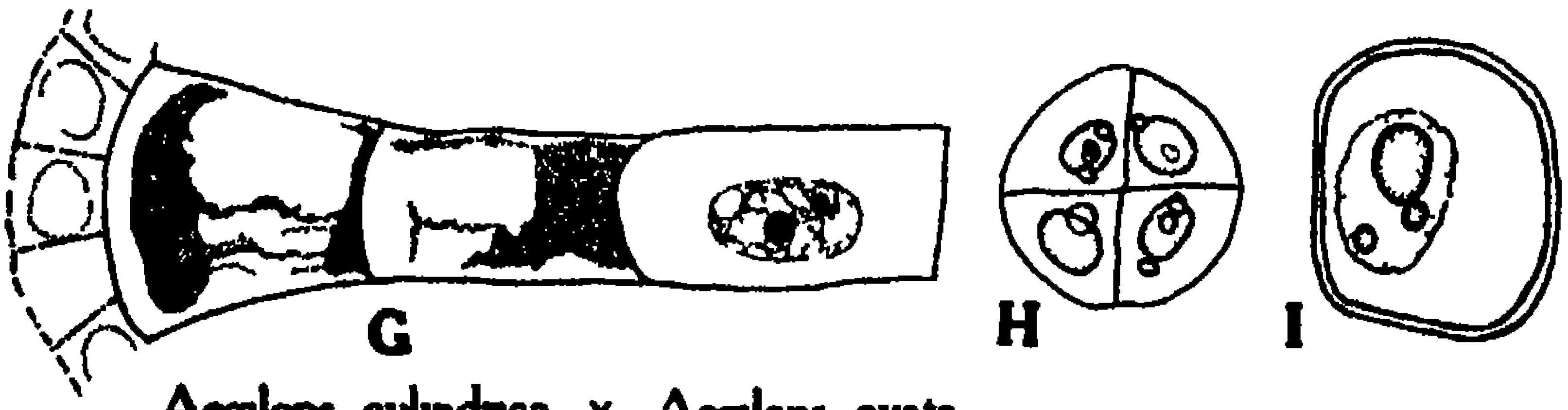
Fig 16 Tetraploids A O diads tetrads and pollen grains X 650



Aegilops cylindrica



Aegilops ovata



Aegilops cylindrica x Aegilops ovata

Fig 17 Tetraploids A-I diads tetrads and pollen grains X 650

Aegilops hybrids investigated by him 'It was rather astonishing that the species hybrids of Aegilops showed also high sterility (Table 9) " According to the table presented by Kihara, the sterility of the 14 + 14 Aegilops tetraploids is on a par with the sterility of the Aegilops-wheat tetraploids, which is very high as compared with that found by numerous investigators for 14 + 14 wheat tetraploids Evidently the relationship in Aegilops species is more complicated than in the cultivated wheats More extensive hybridization within this genus may disclose valuable information bearing on phylogeny in cereals

The tetrad development in the ovules of *Ae ovata* and *Ae cylindrica* (Fig 17 A-D) has been investigated, and found to proceed as in wheat Likewise the heterotypic conjugation is approximately as regular as in the wheat species examined (Fig 13 and Table 10)

The usual chromosome behavior in the first meiotic division of the tetraploid Aegilops hybrids is puzzling The number of trivalents per cell in *Ae cylindrica* x *Ae ovata* is 2, or almost seven times the average found in any of the other hybrids examined (Table 10) This suggests a semi-triploid nature of the hybrid, and a true tetraploid nature of one of the parents *Ae cylindrica* in crosses with vulgare and emmer has two unlike chromosome sets (c7 + d7) The tetraploid nature must be attributed to *Ae ovata*

IV PENTAPLOIDS

(a) *Wheat Pentaploids*

Table 7 Number of Conjugates in Wheat Pentaploids

Hybrid	Range	Mode	Author	Year
T compactum (Hybrid 143) (21) x *T durum* (Kubanka) (14)		14	Sax	1922
T vulgare (Amby) (21) x *T durum*		"	"	"
T durum x *T vulgare* (Amby)		"	"	"
T durum x *T vulgare* (Bluestem)		"	"	"
T vulgare (Bluestem) x *T durum*		"	"	"
T vulgare (Bluestem) x *T turgidum* (Alaska) (14)		"		"
T durum x *T vulgare*		14	Kihara	1924
T polonicum (14) x *T spelta* (21)		"	"	"
T turgidum x *T compactum*		"	"	"
T polonicum x *T compactum*		"	"	"
T durum x *T vulgare*	13 14*	14	Kihara & Nishiyama	1929
T durum (Kubanka) x *T vulgare* (Marquis)	12-14	14	Aase	1930

* Including occasionally 1 or 2 trivalents

As table 7 shows, 14 bivalents are undoubtedly the mode in the pentaploid wheat hybrid Close searching for irregularities will usually result in finding such, and as irregularities occur in species which, for a few generations at least, have not been subjected to cross-breeding, it is not surprising that some irregularities may be found in this cross, but rather a wonder that so few are found Kihara reports occasional trisomes accompanied by a corresponding reduction in the number of univalents, and he finds also, though rarely, 9 univalents The writer has observed some atypical combinations of 3, or even 4 chromosomes (Fig 23 a, b) Such combinations may be a cause for chromosome and genetic discrepancies of later generations Open bivalents occur at the rate of about 3 per cell, a little higher than in the 14 + 14 wheat tetraploids (Table 10) The univalents tend to scatter over the spindle in both ovule and anther (Fig 18 A, B)

Following the disjunction of the bivalents, none to all of the univalents divide equationally, giving a varying number of chromosomes to each daughter nucleus The two chromosome sets a7 and b7 should be represented in each of the daughter nuclei of the diad except when unusual chromosome combinations as trisomes and tetrasomes interfere The final result in the gametes, and possible recovery of the vulgare number, must depend on a fortuitous division of the univalents in the second division as well as in the first

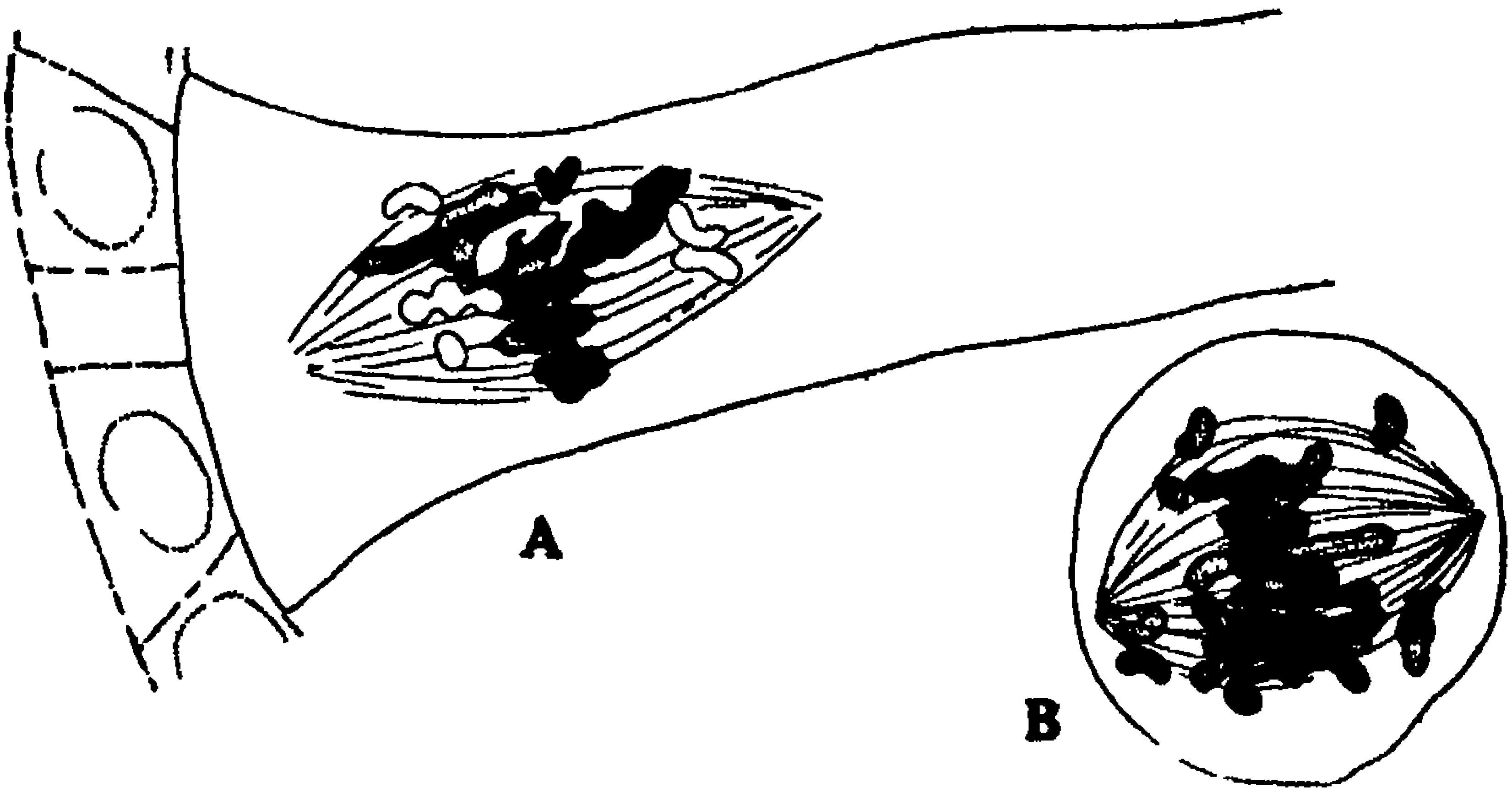


Fig 18 Wheat pentaploid first meiotic division Triticum durum (14) x T vulgare A megaspore mother cell The somewhat irregular arrangement of the 14 bivalents may be the result of sectioning (Unshaded chromosomes from upper section) B typical arrangement of chromosomes 7 univalents and 7 closed and 7 open bivalents X 1800

Anther tetrads and subsequent pollen grains are comparatively regular, but one or sometimes two small nuclei, indicating straying univalents, are usually found in addition to the major nucleus (Fig 25 B, C) The ovule tetrad observed appears to be regular (Fig 25 A)

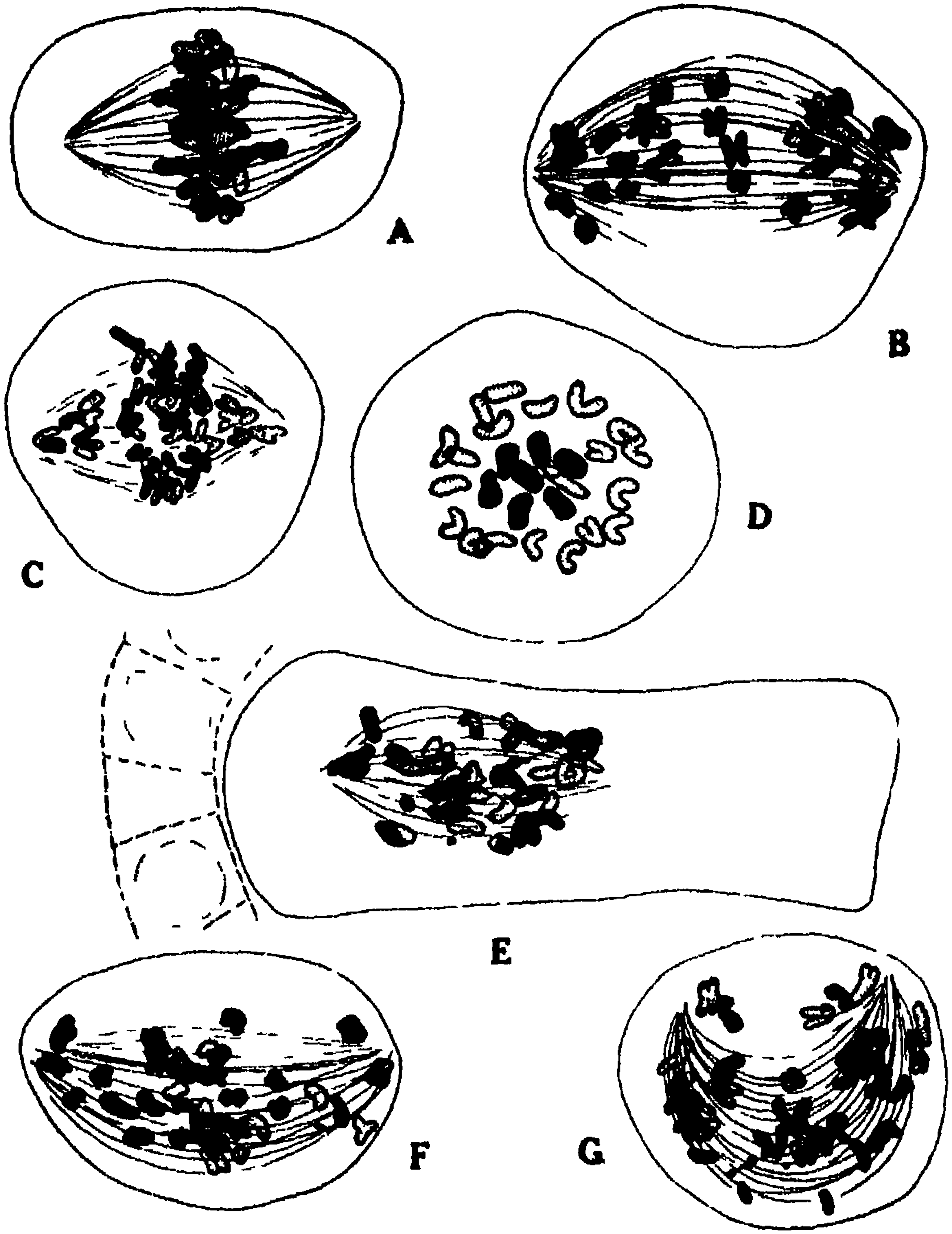


Fig 19 Aegilops wheat pentaploids first meiotic division Aegilops cylindrica (14) x Triticum vulgare (21) typical metaphase side view 14 univalents 5 closed and 2 open bivalents B anaphase All univalents and members of disjoined bivalents have split equationally and 4 univalents lying at the equatorial plate position will probabaly divide C same stage as B but showing most of the univalents dividing

D Ae cylindrica x T spelta (21) metaphase polar view 7 bivalents and 21 univalents slightly more irregular than when T vulgare is the wheat parent E This megaspore mother cell illustrates the irregular formation of univalents bivalents and trivalents frequently observed in the spelt cross F metaphase equational split occurring in all chromosomes G slightly irregular anaphase some univalents dividing X 1300

(b) *Aegilops-wheat Pentaploids*

TABLE 8 NUMBER OF BIVALENTS IN AE CYLINDRICA-WHEAT PENTAPLOIDS

Hybrid	Range	Mode	Author	Year
Ae cylindrica (14) x *T vulgare* (Marquis) (21)	5 7	7	Sax & Sax	1924
T vulgare (Hussar) x *Ae cylindrica*		7	Gaines & Aase	1926
Ae cylindrica x *T spelta*		7	Bleier	1927
T vulgare (Komaba No 3) x *Ae cylindrica*	6 7	7	Kagawa	1928
T vulgare (U A C No 1) x *Ae cylindrica*	6 7	7	"	"
Ae cylindrica x *T spelta*	5 7	7	Bleier	1930
Ae cylindrica x *T vulgare* (Hussar)	6-9	7	Aase	"
T spelta (Alstroum) x *Ae cylindrica*	4-8	7 6	"	"
Ae cylindrica x *T vulgare* (Bluestem)		7	"	"
Ae cylindrica x *T vulgare* (Martin)		7	"	"

Two types of gamete combinations should be possible in producing Aegilops-wheat pentaploids namely wheat 14 + Aegilops 21 and Aegilops 14 + wheat 21 Only the latter of these combinations is described cytologically On the basis of cytological data the wheat-Aegilops pentaploids of this latter group, thus far studied, subdivide into two rather distinct divisions, the *Ae cylindrica* vulgare pentaploids with remarkably constant 7 bivalents + 21 univalents in contrast to the *Ae ovata-* or *Ae triuncialis*-vulgare pentaploids with no bivalents, or a highly fluctuating number of open bivalents That there exists a distinct natural division may be observed by comparing the results in table 8 and table 9

In respect to regularity of pairing and the high proportion of closed pairs the *Ae cylindrica* vulgare group resembles the emmer-vulgare pentaploid decidedly more closely than it resembles the other Aegilops-vulgare pentaploids (Fig 23, Fig 24, Table 10)

The *Ae cylindrica-* vulgare hybrid shows a strong tendency to form equatorial plates, the 7 bivalents occupying the center and the 21 univalents the periphery of the plate (Fig 19 A, D) The univalents may however, be scattered over the entire spindle, and more often so when spelt is the wheat parent (Fig 19 E, F) Spelt, when used as the wheat parent, seems to give rise to more irregularities in general The bivalents are less uniformly 7 in number, and a larger proportion of the bivalents are of the open type Trisomes, rarely found if a variety of *T vulgare* is the wheat parent, are observed at the rate of one in 0 3 of the cells in the spelt-Aegilops cross This is a higher frequency than has been observed in any cross outside of *Ae cylindrica* x *Ae ovata* (Table 10)

Disjunction of the bivalents takes place normally The univalents may go to the poles at random The equational split may, however, overtake them at any location on the spindle, and consequently if many univalents are at the equator at this critical time many univalents will divide as in figure 19 C, but if few univalents are at the equator, as in figure 19 B, few univalents will divide In figure 19 F the equational split has preceded the disjunction of the bivalents The chromosome fragments shown in figure 19 E, G, illustrate further the type of irregularities occurring when the 21-chromosome wheat parent is spelt

The tetrads and pollen grains are very variable as to number and size of cells, and number of nuclei in each cell (Fig 25 D-G, Fig 26 A-D)

TABLE 9 NUMBER OF CONJUGATES IN AEGILOPS-WHEAT PENTAPLOIDS, EXCLUSIVE OF AE CYLINDRICA

Hybrid	Range	Mode	Author	Year
Ae ovata x *T vulgare* (Starling)	0-?	0	Percival	1926
Ae ovata x *T vulgare*	0-3	0	Bleier	1927
T spelta x *Ae triuncialis*	0 5*	0,1 2*	Kihara	1929
Ae triuncialis x *T spelta*	0 7*	1 2,3*	"	"
Ae triuncialis x *T vulgare*	0-5*	1,2 3*	"	"
Ae ovata x *T compactum* (Hybrid 128)	0-3	0	Aase	1930
Ae ovata x *T spelta* (Alstroum)	0 3	1,2	"	"
Ae triuncialis x *T vulgare*	0-3	0 1 2	"	"

* Including trivalents

In contrast to the *Ae cylindrica*-vulgare pentaploids, the *Ae ovata*-vulgare and *Ae triuncialis*-vulgare show only a very low average number of pairs per cell and the pairs present are invariably of the open type (Fig 24, Table 10) Trivalents are again more frequent if spelt is the wheat parent The number of bivalents in the ovules examined lies nearer the maximum as found in the anthers of the cross (Fig

20 A, Fig 21 A) The spindles are elongated and dotted with univalents as is typical in the wide crosses with few conjugates In contrast it may be noted that the *Ae cylindrica*-vulgare ovule containing conjugates (Fig 19 E) presents a spindle of more normal proportions even with the disturbing spelt as the wheat parent In the absence of

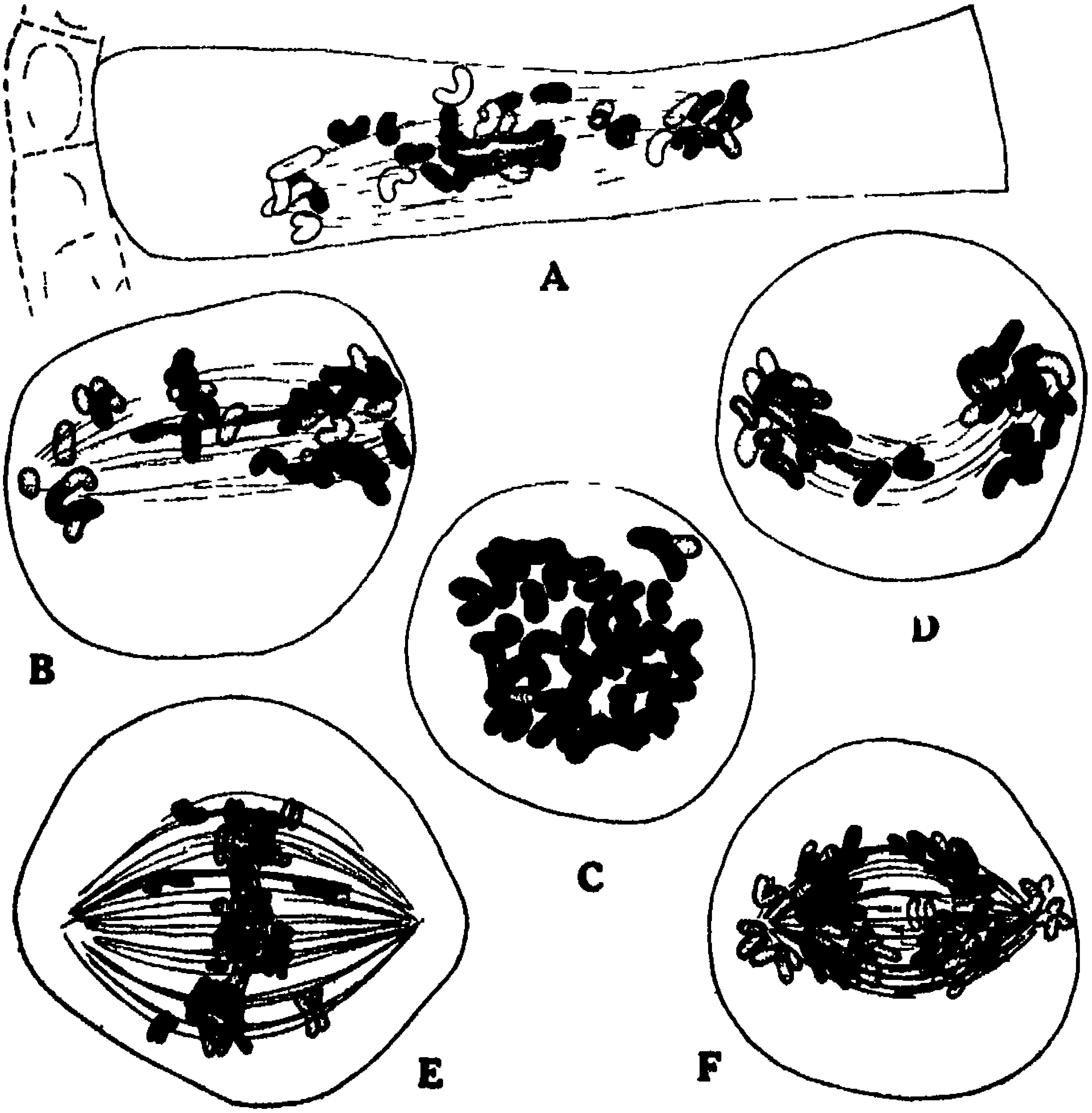


Fig 20 Aegilops wheat pentaploid first meiotic division Aegilops ovata (14) x Triticum vulgare (21) A megaspore mother cell 29 univalents and 3 open bivalents The dispersal of the univalents over the elongated spindle is typical of the cross (Un shaded chromosomes from upper section) B 33 univalents and 1 bivalent C the equatorial plate formation rarely observed in the cross D anaphase showing the random migration of the univalents to the two poles Equational splitting is not evident E an anaphase quite the reverse of that in D the equational splitting having occurred before components of the bivalents have separated The univalents are arranged about as in C F a later stage of a state similar to E The undivided chromosomes at the poles indicate that these were not at the equatorial plate when the splitting occurred, and hence prevented the complete non reduction of univalnts X 1300

closed conjugates there are evidently forces of dispersion which are not counterbalanced by forces of attraction

In the pollen mother cells the spindle may extend as far as the diameter of the cell will allow (Fig 20 B, Fig 21 B), or it may curve to such extent that it parallels the greater part of the circumference of the cell (Fig 22 B) Figure 21 C shows still further spindle exten-

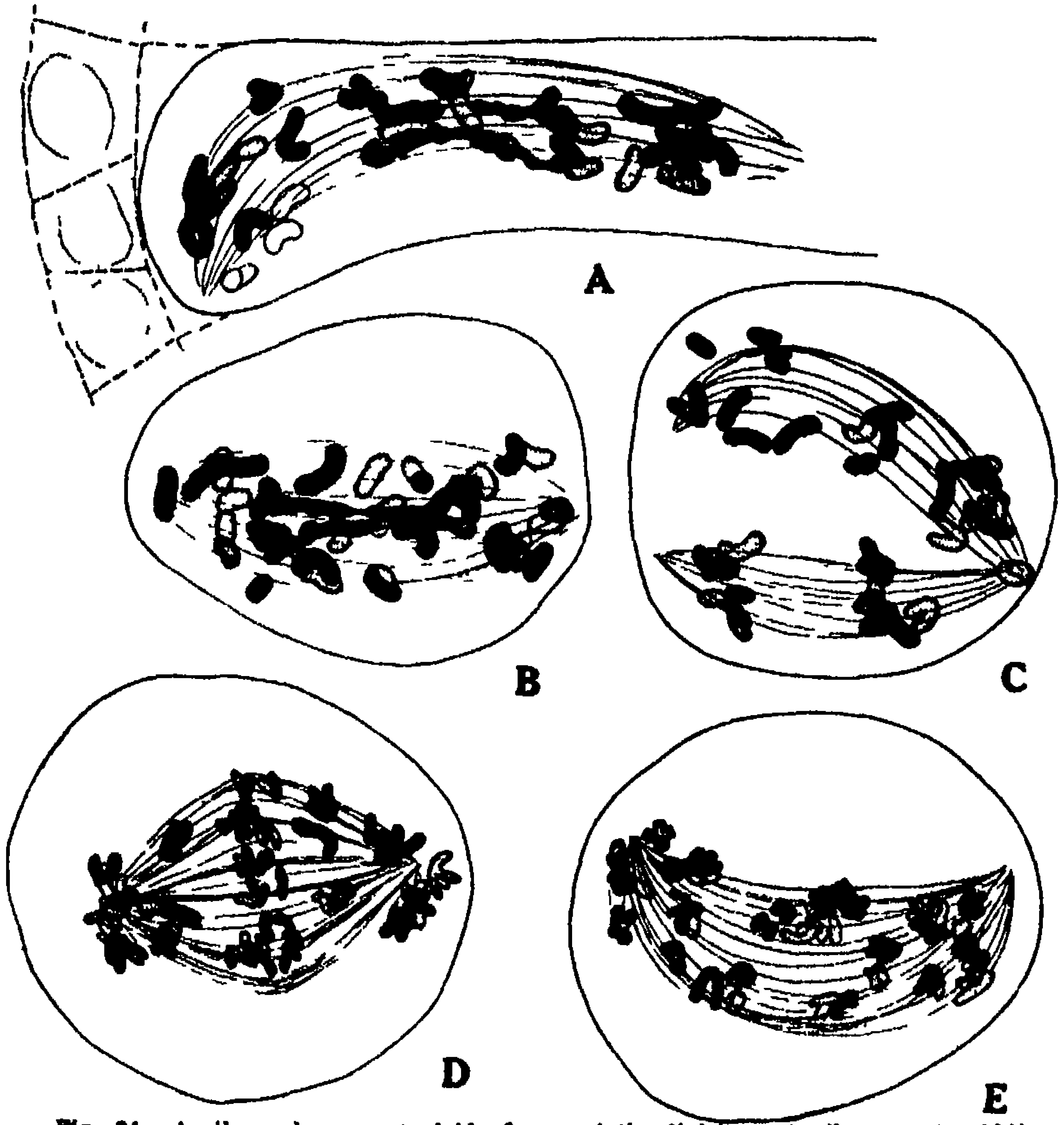


Fig 21 Aegilops wheat pentaploid first meiotic division Aegilops ovata (14) x Triticum spelta (21) A megaspore mother cell 3 open bivalents 29 univalents distributed over the greatly extended spindle (Unshaded chromosomes from other section) B 31 univalents and 2 open bivalents C semi divided spindle one wing bearing approximately 14 chromosomes and the other 21 one chromosome being located at the common pole D many of the univalent chromosomes dividing equationally as a result of their equatorial position at the time the anaphase split occurred E equational split occurring on spindle of type in A and B Few of the univalents will divide equationally X 1800

sion through division into two wings As noted in the tetraploids (Fig 9 F, Fig 11 B, E) the number of chromosomes apportioned to the two wings approximates the number contributed by the respective parents In the tetraploids the numbers are 14 and 14 and in the pentaploids 14 and 21 However, as suggested before, the number of split spindles observed is too small to allow of any interpretation other than coincidence The anaphase events parallel in general the description of the preceding crosses To sum up there is correlation in time between

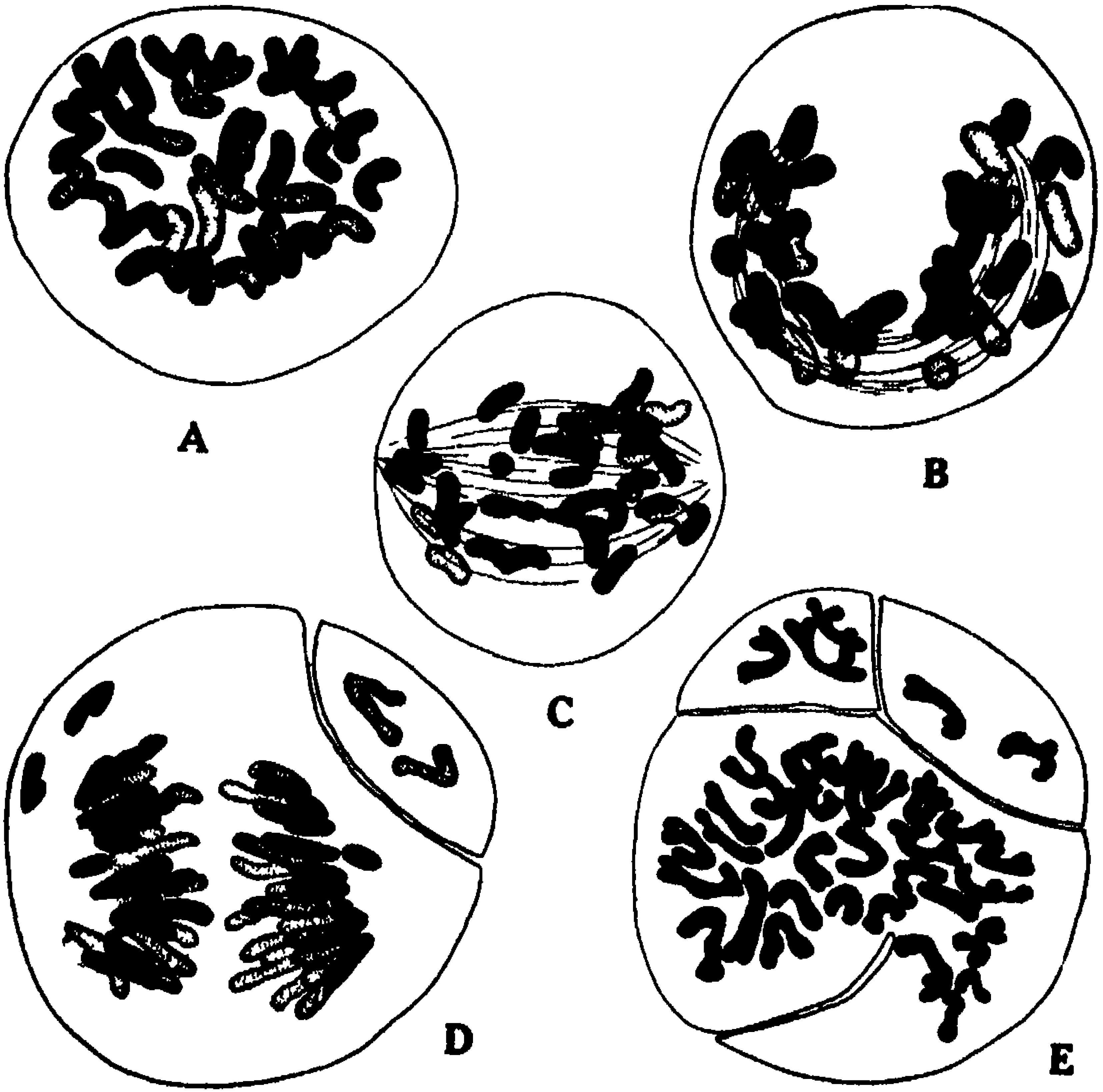
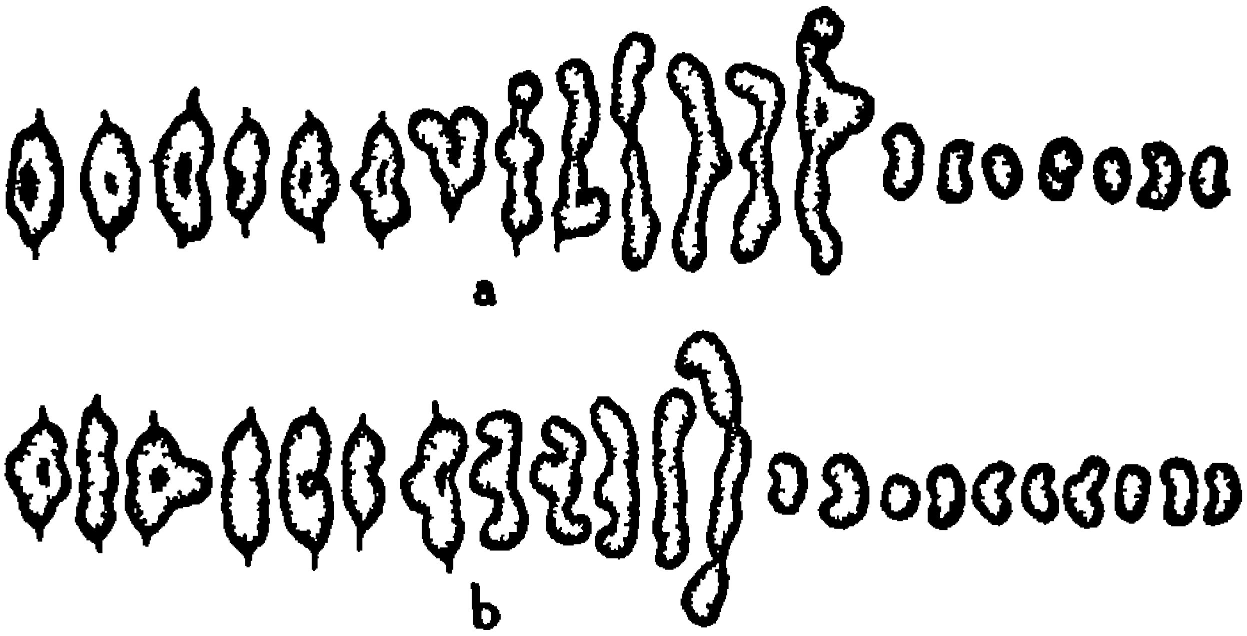
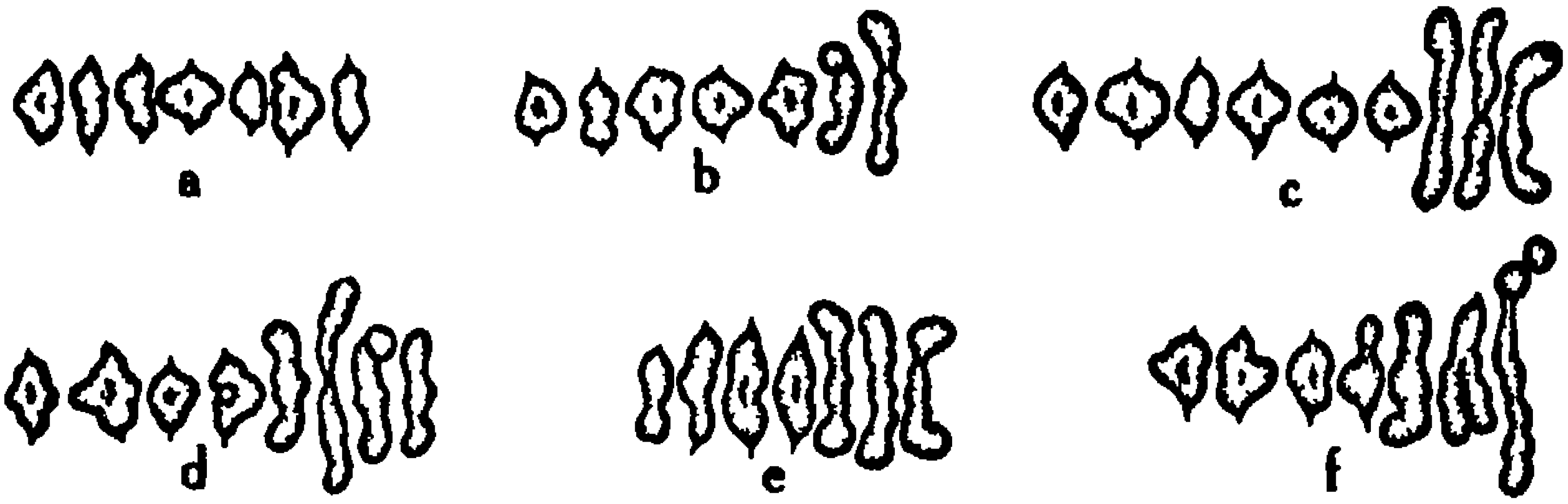


Fig 22 Aegilops wheat pentaploid first meiotic division Aegilops triuncialis (14) x Triticum vulgare (21) A metaphase polar view The equatorial plate arrangement of the univalents has been frequently observed in this hybrid B extended and curved spindle and dispersed distribution of univalents C 33 univalents and 1 bivalent D anaphase of a plate formation similar to A Almost complete non reduction of univalents E, late metaphase polar view stage between A and D The unusual cleavage through the periphery of the equatorial plate occurs frequently in this cross indicating possibly a delayed or suppressed metaphase of the first division X 1800

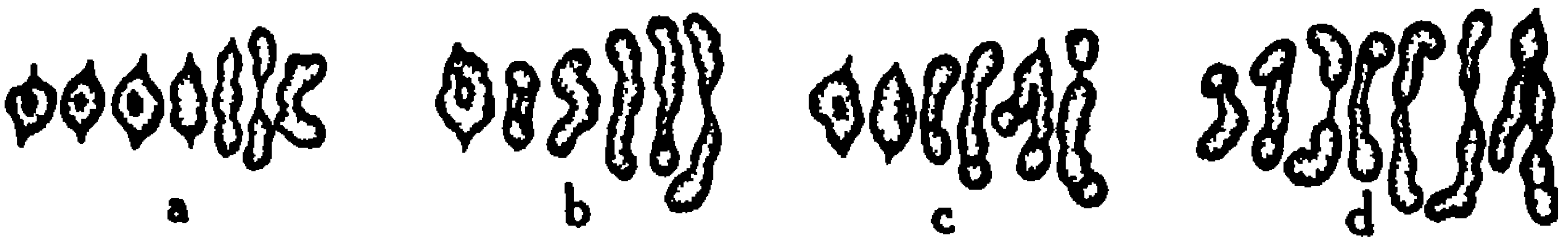
the migration of univalent chromosomes to the poles and the initiation of the equational division of univalents In figure 20 D migration to the poles precedes equational division, and nearly all, if not all, univalents will reach the poles undivided In figures 20 F and 21 D, E migration was preceded by the equational split, and the number of chromosomes that will actually divide equationally in the first division depends on the number located at the equatorial plate In figure 20 E the equational split has preceded even the disjunction of the lone



Triticum durum x Triticum vulgare



Aegilops cylindrica x Triticum vulgare



Triticum spelta x Aegilops cylindrica

Fig 23 Pentaploids chromosome conjugation a, b c etc conjugates of the respective spore mother cells except in the wheat hybrid where the entire chromosome complement of each cell is represented X 1800

bivalent The almost complete plate formation in figure 20 E will, no doubt, lead to the equational division of most of the univalents, but the presence of the members of the bivalent, and a small number of univalents lying off the equatorial plate will probably initiate a second division and thus prevent the non-reduction of univalents

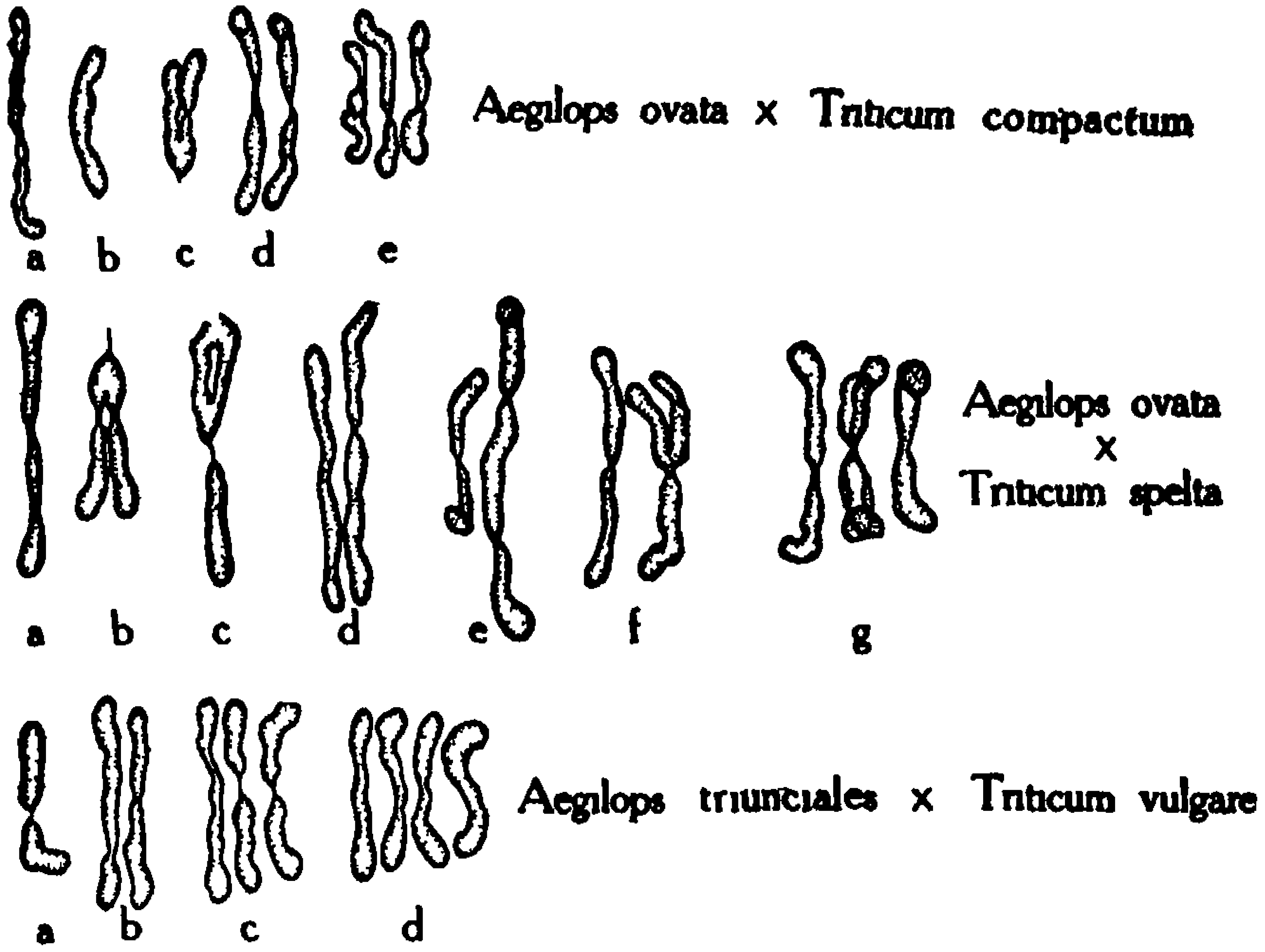
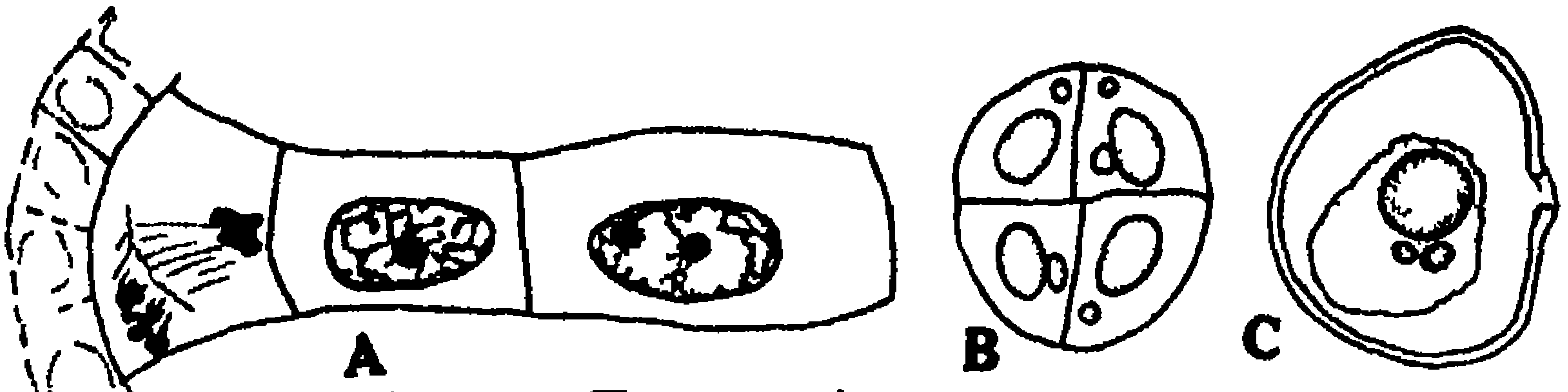

a
b
c
d
e
Aegilops ovata x Triticum compactum
a
b
c
d
e
f
g
Aegilops ovata
x
Triticum spelta
a
b
c
d
Aegilops triunciales x Triticum vulgare

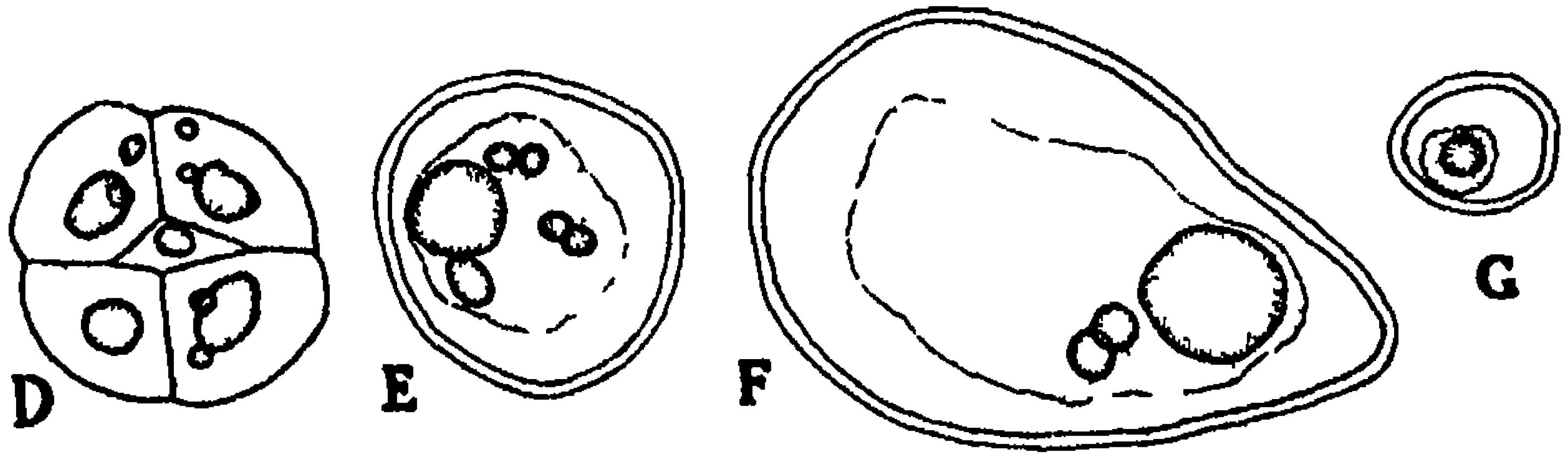
Fig 24 Pentaploids chromosome conjugation a b c etc conjugates from the respective spore mother cells X 1800

While the equatorial plate formation (Fig 20 C) is rare in the *Ae ovata*-vulgare crosses, it has been rather frequently observed in *Ae triuncialis* x *T vulgare* (Fig 22 A, E)

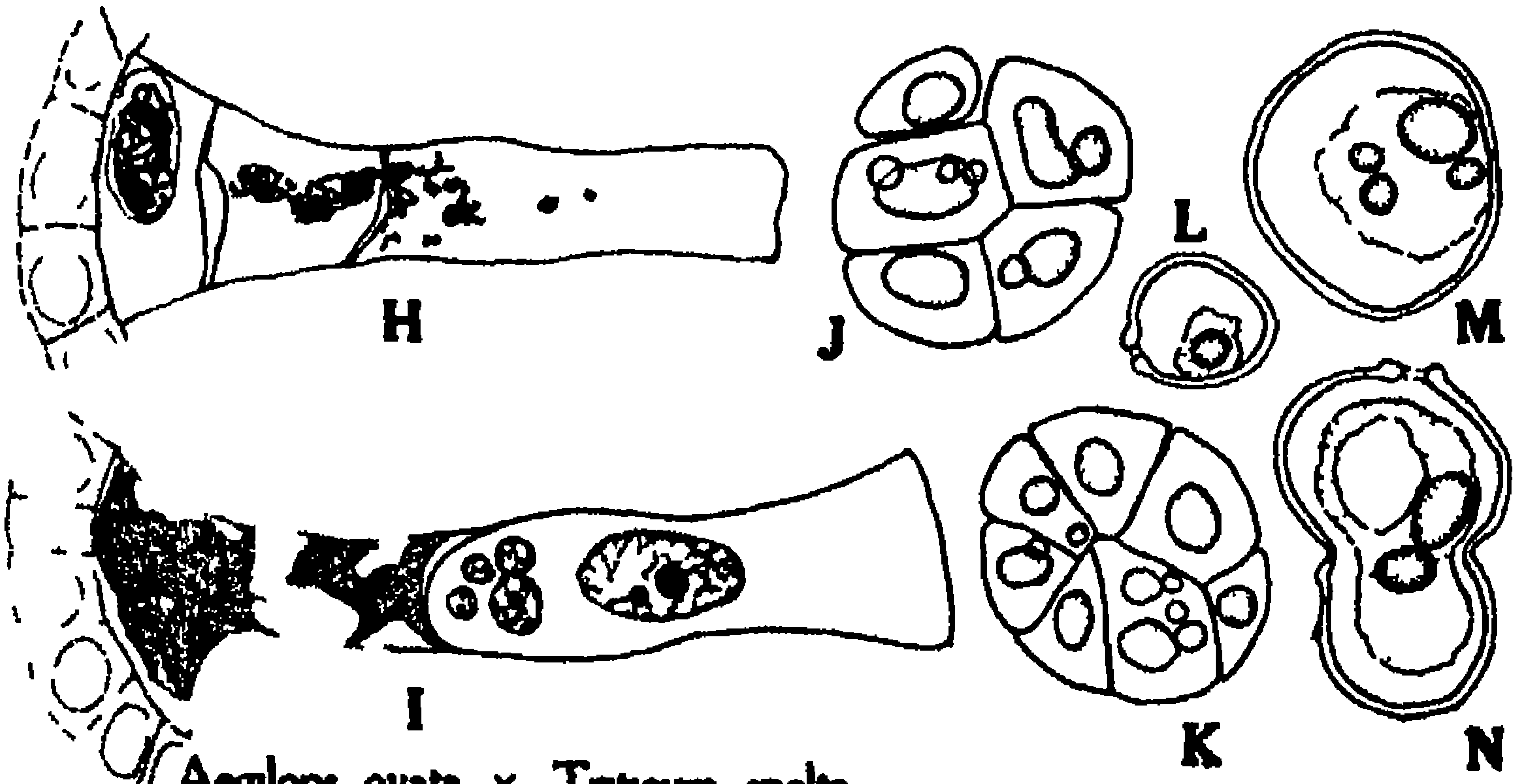
As the 35 univalents located on the equatorial plate are about to divide equationally, cleavage furrows sometimes form in the cytoplasm These cleavage planes may run parallel or perpendicular to the equatorial plate of univalents, and may cut off out-lying chromosomes or, as happens in some instances, merely indent the chromosome group (Fig 22 D, E) This behavior indicates probably either a further hopeless delay of the first division of the spore mother cell, or a premature ushering in of the second division, emphasizing the tendency,



Triticum durum x Triticum vulgare



Triticum spelta x Aegilops cylindrica

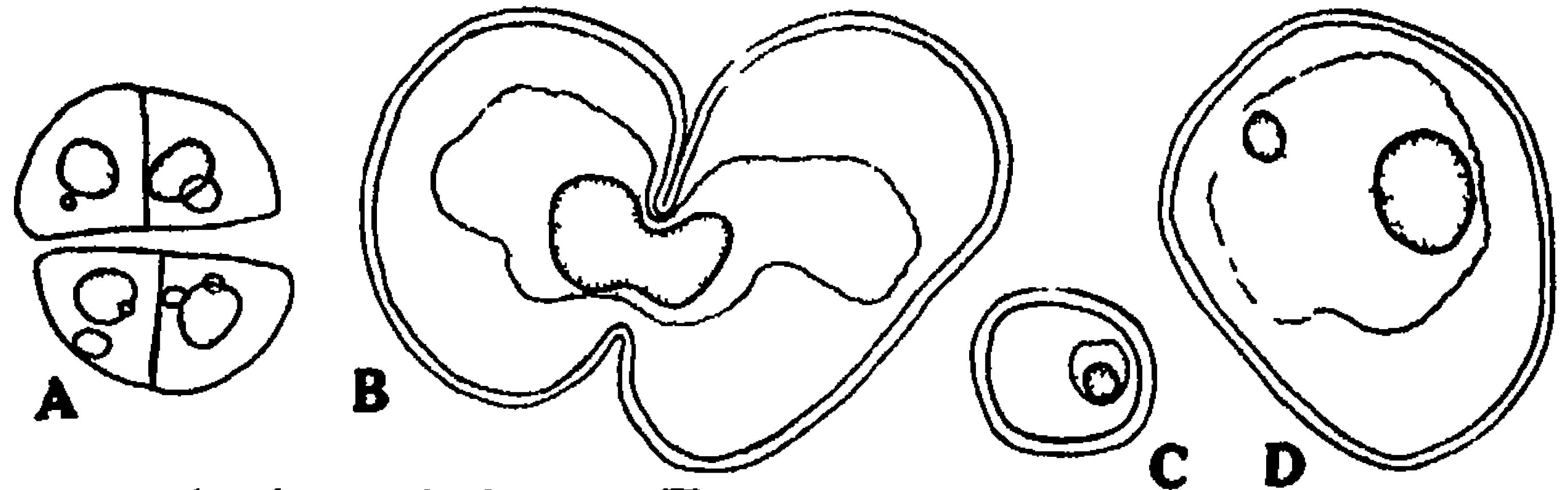


Aegilops ovata x Triticum spelta

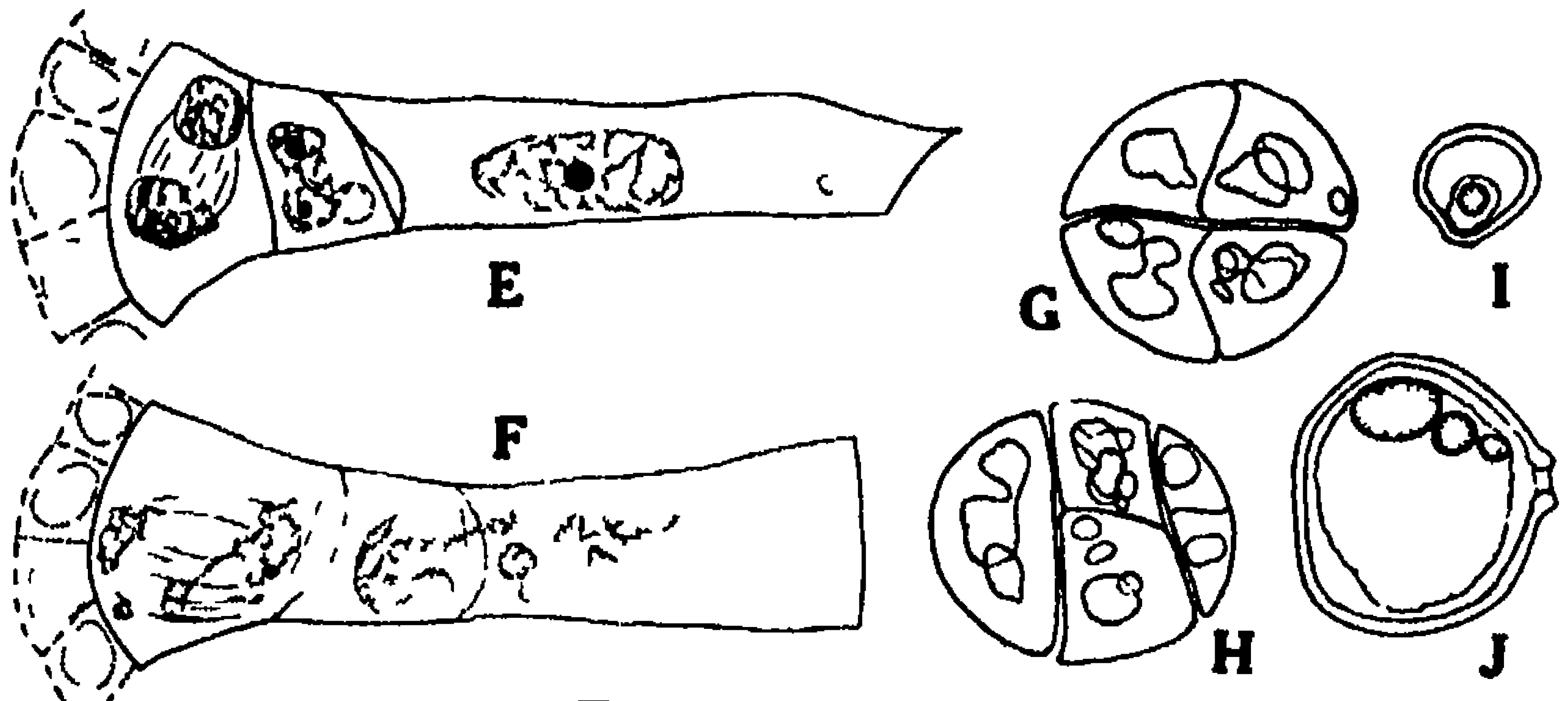
Fig. 25 Pentaploids A–N tetrads and pollen grains X 650

in these hybrids, toward the breaking down of demarcations between the first and second division, or, in other words, a merging of the two divisions.

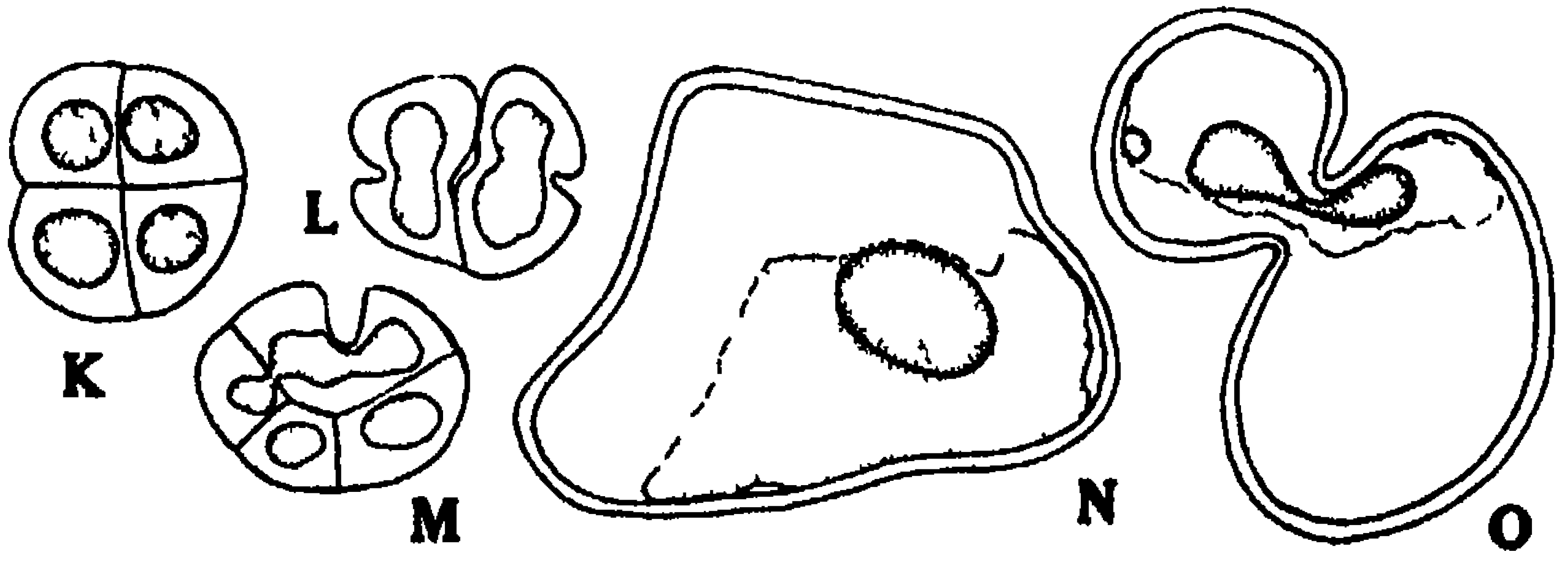
As repeatedly described for these hybrids, reduction of univalents may occur in one or the other of the two divisions, or in respect to different univalents in both. Non-disjunction is generally restricted to the first division, yet the occasional appearance of the equational split before disjunction is (Figs 3 B, 11 G, 12 D, 19 F, 20 E) a further encroachment of one division on the other, and is suggestive, at least, of a step toward the reversal of the two divisions, in respect to reduction, also in case of bivalents



Aegilops cylindrica x Triticum vulgare



Aegilops ovata × Triticum compactum



Aegilops triunciales × Triticum vulgare

Fig. 26. Pentaploids. A-O, diads, tetrads, and pollen grains × 650

The non-reduction of univalents has not been observed to be entirely complete, even in the *Ae triuncialis*-vulgare cross, though figures as 22 D show a close approach, and diads and large pollen grains (Fig 26 L, N, O) point in this same direction

The pentaploid Aegilops-wheat hybrids, as a group, generally give rise to great irregularity of tetrads and pollen grains (Fig 25, Fig 26) Of the four ovules illustrated, two show an impossible state of chromatin in the megaspore ordinarily functioning, and only one of the remaining two (Fig 26 E) compares at all favorably in appearance with the same stage of the pentaploid wheat (Fig 25 A)

V HEXAPLOIDS

Aegilops-wheat Hexaploid

Ae triaristata (21) x *T vulgare* (21), according to Bleier (1930), gives rise at meiosis to 0-7 bivalents The fluctuation in number of pairs which are also illustrated as of the open type suggests a waning chromosome homology

VI SUMMARY TABLE

Table 10 supplements the illustrations which must necessarily be too few to represent the variations that occur in a cross It is also an effort to assemble and correlate otherwise isolated facts Straight species have been included for the sake of comparison

The counts reported are too limited in some hybrids, but are, however, further supported by observation of many other cells rejected because of sectioning or orientation unfavorable to accurate counting In hybrids with a large proportion of univalents, as in rye-wheat, or Aegilops-vulgare, only the conjugates have been checked

VII CONCLUSIONS AND DISCUSSION OF THEIR POSSIBLE BEARING ON PHYLOGENY

1 *In the concluding discussion the hybrids will be arbitrarily classified as diploids, haploids, and semi-haploids* In the diploid class are the hybrids like *T durum* x *T polonicum* with approximately complete chromosome conjugation In these hybrids all the chromosomes are in the diploid state

The haploid class is represented by forms like *T durum* x *S cereale*, and *Ae ovata* x *T vulgare*, with no bivalents or a small fluctuating number of open bivalents While none of these haploids of hybrid origin shows the almost complete absence of bivalents typical for the parthenogenetically developed haploid, yet in meiotic behavior they are indistinguishable from the latter haploid

The parthenogenetically produced haploids of *Solanum nigrum* described by Jorgensen (1928) cannot be included in this classification of haploids, for Jorgensen states *"The reduction division of these haploids thus approaches the type* $12_{II} + 12_{I}$, or, in other words it is similar to the reduction exhibited by many triploids, whether species triploids or hybrid triploids"

Disjunction whereby the like, or only slightly differing, members of a bivalent separate for the respective daughter nuclei is inevitably rare Instead a reduction of the unpaired chromosomes usually occurs in the random movement of these to the poles in the first or second division This reduction is of such a severe and unbalanced nature that it produces results as would an extensive and indiscriminate non-disjunction in diploids That the chromosome complement of the hybrid is in most cases fatally unbalanced is further evidenced by the great sterility of these haploids whether of hybrid or parthenogenetic origin

T durum x *T vulgare* with approximately 14 bivalents and 7 univalents is a representative of the semi haploid class This hybrid is diploid as to 28 of its chromosomes and haploid as to 7 *Ae cylindrica* x *T vulgare* with 7 bivalents and 21 univalents is diploid as to 14 chromosomes and haploid as to 21 In these semi-haploids disjunction of bivalents proceeds normally as in pure species, while the reduction of univalents proceeds approximately as in the haploid class, and sterility increases, though only very generally, in proportion to the increase in univalents over bivalents

As in most natural classifications on whatever bases, there are some borderline or more or less wavering forms So in this classification based on chromosome conjugation there are forms that fail to comply strictly with any one of the above three classifications In these borderline forms the bivalents are almost invari[illegible] of the open type They vary in number from cell to cell, they are more readily influenced by varietal difference of parentage, and also possibly by external factors The results obtained by individual investigations tally less closely in this class of hybrids *Ae ovata* x *T monococcum* is a typical fluctuating type Whether or not the 0-6 open bivalents are the result of autosyndesis, there is in this cross a waning homology resulting in feeble pairing The Aegilops (14)-emmer, and some of the Aegilops (14)-vulgare (*Ae cylindrica*-vulgare excepted) are possibly on the borderline, though very close to the haploid class As may be observed in tables 5 and 9, the numbers of open bivalents are at variance both as to each cross and as to the results of the individual investigators

Einkorn-emmer, hovering around the $7_{II} + 7_{I}$ (Table 1) formula, may still be classed with the semi-haploids, but the decreasing number of closed bivalents, and varying number of bivalents, point to a slipping from the semi-haploid toward the haploid class Einkorn-vulgare, with an average of fewer bivalents, and these of the open type, illustrates still further progress in the same direction

Possibly a fourth class should be added to include *Ae cylindrica* x *Ae ovata* The frequency of trivalents, together with the otherwise irregular pairing, suggests a state of triploidy Perhaps this hybrid is triploid as to 21 chromosomes, and haploid as to 7

2 *Haploids and semi-haploids may be robust individuals indicating a chromosome complement conducive to the harmonious functioning of the somatic activities, but as annuals they fail to propagate themselves vegetatively without artificial aid* The parthenogenetic haploid wheat plant was artificially multiplied by stolons to produce several plants the following year and could no doubt have been thus propagated indefinitely

3 *Haploidy and semi haploidy invariably lead to unbalanced chromosome complements in the gametes, and consequent greater or less sterility* The various types of apogamy that have arisen in some plants compensate, possibly, for a crippled gamete-developing mechanism, such as found in haploids and semi-haploids

4 *Haploidy and semi-haploidy must be changed to diploidy for the proper functioning of the meiotic mechanism, and the propagation of the form*

5 *Haploidy may be changed to diploidy by duplication of the chromosome complement in the somatic tissues* That chromosome doubling can take place in the vegetative cells has been shown conclusively by the experiments conducted by Jorgensen (1928) in the production of tetraploid Solanums Jorgensen states in his conclusions

TABLE 10 CHROMOSOME RELATIONS IN FIRST MEIOTIC DIVISION

Plant	Somatic number	Univalents			Bivalents									Trivalents average	Tetravalents average	Cells counted
					Total number			Closed type			Open type					
		Average	Mode	Range	Average	Mode	Range	Average	Mode	Range	Average	Mode	Range			
Triticum monococcum (Einkorn)	14	0	0*	0	7 0	7*	7	6 8	7*	6-7	2	0*	0-1	0	0	19
Secale cereale (Rosen)	14	1 5	0 2	0 4	6 2	6, 7	5-7	4 9	5 4	3-7	1 3	1 2	0 3	trace	0	21
T durum (Kubanka) x *T monococcum* (Einkorn)	21	9 2	9†	7 13	5 9	6*	4-7	3 2	3	2 5	2 7	2 3	0 5	trace	0	12
T dicoccoides (Wild Emmer) x *T monococcum* (Einkorn)	21	9 4	11 9	7-11	5 5	5,†6	4-7	2 8	2	0-6	2 7	3†	0 5	.2	0	26
Aegilops ovata x *T monococcum* (Einkorn)	21	16 1	19 15	9-21	2 3	1 2 3	0 6	0	0*	0	2 3	1 2, 3	0-6	1	0	88
T durum (Kubanka) x *S cereale* (Rosen)	21	19 8	21† 19	13 21	6	0,†1	0-4	0	0*	0	6	0 †1	0-4	0	0	42
T compactum (Hybrid 128) haploid	21	21 0	21*	21	trace	0*	0 1	0	0*	0	trace	0*	0-4	trace	0	58
T turgidum (Alaska)	28	0	0*	0	14 0	14*	14	13 0	14†	11 14	1 0	0†	0 3	0	0	11
Ae cylindrica	28	0	0*	0	14 0	14*	14	13 1	14, 13	11 14	9	0, 1	0-3	0	0	15
Ae ovata	28	0	0*	0	14 0	14*	14	12 3	12, 13	9 14	1 7	1, 2	0 5	0	0	27
T durum (Kubanka) x *T polonicum* (Polish)	28	7+	0†	0 2	13 6+	14†	13 14	13 0	13†	11 14	6+	0 1	0 2	0	0	11
T durum (Kubanka) x *T dicoccoides* (Wild Emmer)	28	2	0*	0-2	13 1	14†	11-14	11 1	12	8 14	2 0	2	0 5	0	4	21
Ae cylindrica x *Ae ovata*	28	6 9	8	3 10	5 5	7 †3	3 8	1 4	2,†1	0-2	4 1	6	0 6	2	9‡	8
Ae cylindrica x *T durum* (Kubanka)	28	25 3	26 28	18 28	1 2+	1 0	0 5	trace	0*	0 2	1 2+	1 0	0 5	trace	0	76
Ae cylindrica x *T turgidum* (Alaska)	28	26 2	28 26	20-28	9	0,†1	0 4	trace	0*	0 2	9	0 †1	0-4	trace	0	76
Ae ovata x *T durum* (Kubanka)	28	26 6	26 28	22 28	7	1 0	0 3	0	0†	0	7	1 0	0 3	1—	0	55
T vulgare (Triplet) x *S cereale* (Rosen)	28	26 8	28 †26	22-28	6	0 †1	0 3	1+	0*	0 2	4+	0 †1	0 2	trace	0	55
T spelta (Alstroum x *S cereale* (Rosen)	28	26 6	28 26	20 28	7	0 1	0-4	0	0†	0	7	0 1	0-4	trace	0	50
T durum (Kubanka) x *T vulgare* (Marquis)	35	7 4	7*	7 11	13 8	14†	12-14	10 6	9 10 11	8 14	3 2	2 4 5	0 6	trace	trace	13
Ae cylindrica x *T vulgare* (Hussar)	35	20 9	21†	17 23	7 0	7†	6 9	5 7	5 6 7	3 7	1 3	1 2	0 4	trace	0	34
T spelta (Alstroum) x *Ae cylindrica*	35	21 7	21 †23	19 25	6 1	7, 6	4 8	2 6	3 2	0 3	3 5	3 4	0 6	3	trace	20
Ae ovata x *T compactum* (Hybrid 128)	35	34 6	35*	29 35	2	0*	0-3	0	0*	0	2	0*	0 3	trace	0	76
Ae ovata x *T spelta* (Alstroum)	35	32 3	33 31	28 35	1 2	1 2	0 3	0	0*	0	1 2	1 2	0 3	1	0	40
Ae triuncialis x *T vulgare* (Hussar)	35	32 6	33, 35, 31	31 35	1 2	1 0 2	0-3	0	0*	0	1 2	1 0 2	0 3	0	0	65
T vulgare (Turkey Red)	42	4	0*	0-2	20 8	21*	20-21	19 6	20, 19	17-21	1 2	1†	0-4	0	0	28

* Occurs in 75% or more of cells
Number representing strongest mode precedes
Traces may or may not be included in cells counted

† Occurs in 50% or more of cells
‡ And less frequently larger conjugates

"The majority of the polyploid forms, however, in my opinion owe their origin to doubling processes ('endo-duplication,' p 155) in the somatic tissue Considering the widespread occurrence of binucleate cells in the soma and the continuous somatic development of most plants, it is only natural that endo-duplication must be an important factor in the formation of polyploid plants It is true that repeated doubling will give rise to an *n*, 2*n*, 4*n*, 8*n* series, but the missing types can be easily imagined to result from the combination of doublings with intercrossing of the types Because the polyploid individuals have originated from diploid ones, they will usually be found as a few individuals in populations of these, and have much opportunity of being back-crossed The formation of a triploid shoot from a diploid tomato stock (p 156) may also be recalled here" Experiments, such as Jörgensen has carried on in the Solanums, might be undertaken in cereals Many of the hybrids produce stolons very freely Doubling of the chromosome complement has been observed, by the writer, in individual cells of the somatic tissue of anthers and ovules of cereals and their hybrids, but has not been found to involve larger areas

6 *Haploidy may be changed to diploidy in the meiotic divisions through non-reduction of the univalents* As stated before, reduction as related to the univalents of the haploid is severe and unbalanced leading to sterility If reduction of univalents could be suppressed in both meiotic divisions, the resulting gametes would retain the complete chromosome complement of the hybrid This result might be accomplished through the inclusion of all the univalents on the equatorial plate, followed by their complete equational division in one division of the spore mother cell, that division representing a merging of the two normal meiotic divisions This method has been referred to in this article as non-reduction of univalents

That there is a strong tendency to merge the two meiotic divisions in these hybrids is shown repeatedly by the equational division affecting the univalents in the first division, in some cases even before disjunction of bivalents, and in *Ae triuncialis* x *T vulgare* by the appearance of the wall formation before the completion of either division In the cereals the wall formation usually follows very promptly the first meiotic division, so that, unless it strikes large chromosome masses, it precludes the union of the two daughter nuclei into a large nucleus for the second division

The fact that the parthenogenetic haploid wheat produced 9 normal diploid plants is strong evidence for an egg nucleus containing the entire 21-chromosome complement of the haploid. The comparatively large number of normal diploid seeds produced by the hybrids of parthenogenetic origin, may possibly be explained as due to open fertilization by vulgare pollen. As yet no conclusive evidence has been found to support the theory that non-reduction of the univalents is the cause of a 21-chromosome embryo sac of the haploid wheat. Yet meiotic figures (Fig. 3 EE_1 and Gaines and Aase, 1926, Fig. 5 D) point strongly in that direction in both ovules and anthers. The complete non-reduction of all the univalents has not been found. Figure 5 J indicates that the inner cell of a diad is enlarging in preparation to form the embryo sac.

Many plausible schemes to account for the production of polyploid gametes are well illustrated and discussed by Rosenberg (1926), Matsuda (1927), Brieger (1928), Karpechenko (1927), and Tschermak (1929). Some of these may be found applicable to cereals. At the present state of progress of this investigation, the writer has been impressed by the frequent non-reduction of univalents in the first division. This non-reduction varies in degree, in observed cases, so as to involve only few univalents or to include almost the entire number. Fusion of nuclei of pollen mother cells in the first meiotic division was observed in anthers of the haploid wheat by Gaines and Aase (1926), but such fusion in anthers cannot account for the 21-chromosome gamete in the ovule.

That haploidy may change to diploidy, not only in haploids of parthenogenetic origin, has been clearly demonstrated by the experiments conducted by Karpechenko (1927). The fertile tetraploid *Raphanus-Brassica* (18R + 18B) arose in the F_2 progeny of *Raphanus sativus* x *Brassica oleracea* (9R + 9B) through the formation, in the meiotic divisions, of gametes with the somatic chromosome complement of the F_1. The Aegilotricum tetraploid discovered by Tschermak and Bleier (1926) as a fertile stable form in the F_2 and F_3 progeny of *Ae. ovata* x *T. dicoccoides* and *Ae. ovata* x *T. durum*, though it fails to give information as to its exact origin, nevertheless shows without doubt, that fertile diploid forms may arise as progeny of haploid hybrids.

7. *Bivalents and larger chromosome conjugates are probably a source of interference to non-reduction of univalents.* Non-reduction

of univalents, must be complete in the first and only meiotic division, if it is to produce gametes with the entire chromosome complement of the haploid or semi haploid If bivalents are present, and non-reduction occurs in the first division, the presence of the members of the disjoined bivalents, evidently, initiates a second division, during which the halves of the univalents will be subject to reduction unless these again divide

Diploidy is, however, acquired in semi-haploids, as evidenced by the emmer-vulgare and vulgare rye crosses in which some of the progeny recover the diploid number of the vulgare parent That complete diploidy of the univalents may be acquired in semi-haploids when both parents have, supposedly, contributed to the haploidy, as in the case of *Ae cylindrica*-vulgare, has, to the writer's knowledge, not yet been shown in the cereals

8 *Chromosome homology is subject to change* That chromosomes of a hybrid retain their homology for the respective chromosomes of the parents has been proved by back-crossing Sax (1927) back-crossed the F_1 hybrid *Ae ovata* x *T dicoccum* with *T dicoccum* and noted in the meiosis of the F_1 14 bivalents The 14 bivalents illustrated are the closed type, and not the end-to-end type characteristic of the few bivalents occurring in the *Ae ovata* x *T dicoccum* F_1 There seems little doubt that close pairing indicates a homologous state of chromosomes, and that this homology may be retained by the respective chromosomes, even when in combination with foreign chromosome sets more or less different in genic constitution, and even morpholology, as occurs in wide crosses The nature of the affinity between pairing mates is, as yet, unexplained There evidently exists a close relation between pairing affinity and genic homology of pairing mates The equational splitting of a chromosome results in the maximum pairing affinity, as well as in the maximum genic homology of pairing mates in the chromosome-descendents of the halves Belling and Blakeslee (1926) concluded that in *Datura* pairing may take place between like ends of otherwise non-homologous chromosomes

That changes may occur in genes, either as losses or additions, has been demonstrated through breeding experiments It seems logical to assume that the affinity of homologous mates will likewise change, from time to time, as the generations pile up behind the offspring of a hybrid The homologous state of the chromosomes changes both in the parents and in the progeny of the hybrid, so that back-crossing with the parents if it could be accomplished intermittently throughout countless generations, would show increasingly feebler pairing The feebler pairing would manifest itself progressively by a smaller average number of pairs, a larger proportion of the loose end-to-end type, greater fluctuations in number, possibly influenced by external conditions, and eventually by the almost complete disappearance of pairs Changes in chromosome affinity must go hand in hand with changes in the genic constitution of chromosomes, and also, no doubt, with changes in chromosome morphology It would be folly to assume that these changes take place simultaneously in all the chromosomes of a cell, or in all the homologous chromosomes in the race It is rather to be assumed that each genic change, or any change in pairing affinity, is extremely independent as to the individual chromosome affected, the part of the chromosome affected, and as to time Thus, in homologous chromosome sets, whether these constitute the nuclear complement of an autopolyploid (with like sets of 7) or a heteropolyploid hybrid (with unlike sets of 7), or of a primary species, changes in genes in pairing affinity and in chromosome morphology occur hit and miss throughout the generations of respective progeny

As back-crossing of isolated offspring of hybrids and of primary species becomes increasingly difficult, it may be imagined that pairing affinity may still persist between some of the formerly homologous mates and that under propitious conditions conjugation will take place Likewise some genes may persist more or less unchanged, and show up as factor duplications in the hybrid or back-cross Some chromosomes may have eluded the morphological changes of homologues more than others and may, hence, more readily be identified as homologues in the progeny The allelomorphism, thus brought about, forms in its earlier stages the basis for the production of new combinations through hybridization Eventually, it may be logical to assume that genic changes have so affected the protoplasm of the isolated offspring, whether of species, or of polyploid hybrids, that pollen tubes fail to grow on the stigma, or fertilization for some other similar reason fails to be accomplished To date, no crosses have been obtained beyond taxonomic genera in plants Hybridization or back-crossing must be accomplished before this critical point has been approached

To summarize, non-reduction, or equational division of univalents, brings about diploidy and its consequent homology of mates The homologous mates thus formed tend infinitely to vary, however minutely, as they are passed on through the progeny, and whether they lie in the nucleus of a primary species, or of a polyploid hybrid The equational division of univalents produces homologues and favors species-stability The ever present tendency on the part of homologues, to change favors species-splitting Hybridization combines or redistributes the changed homologoues The tendency to change is perpetual, hybridization is usually spasmodic

9 *The vulgare wheats and Aegilops cylindrica are hybrids of comparatively recent origin* Gaines and Aase (1926) proposed a hypothetical scheme to show the relationship between some species of wheat and Aegilops Considerable work in the cytology of wheats and Aegilops and hybrids of these, has been done since that time, both by the writer and others But these investigations are still too fragmentary to warrant positive conclusions However, the piecing together of these fragments has not yet suggested a better substitute for the proposed hypothesis, as far as it goes and it is easy to yield to the temptation to piece the fragments still farther and propose, as continuation, the hypothetical scheme in figure 27

That 14 bivalents occur in emmer-vulgare, and 7 in *Ae cylindrica*-vulgare, has been illustrated repeatedly The bivalents are remarkably stable in number and predominantly of the closed type in both crosses When *Ae ovata* or *Ae triunciales* is used in place of *Ae cylindrica,* none or few bivalents occur, and these when occurring, are of the open type These facts set *Ae cylindrica* apart from the other species of Aegilops, thus far used, in crossing with vulgare wheats If however, *Ae cylindrica* is crossed with emmer, the results are approximately the same as when *Ae ovata* or *Ae triuncialis* is crossed with emmer The bivalents are none or few, and of the open type

The constant number of closed bivalents in the emmer-vulgare indicates recent hybrid origin of vulgare, involving emmer as one parent Likewise, the constant number of closed bivalents in the *Ae cylindrica*-vulgare cross indicates recent hybridization, involving one set of 7 chromosomes from *Ae cylindrica* In other words, the chromosome sets *a* and *b* from emmer, and set *c* from *Ae cylindrica,* compose the chromosome complement of vulgare wheats It is doubtful that the vulgare wheats have resulted from the hybridization of *Ae cylindrica* by emmer It is more probable that *Ae cylindrica* and vulgare have one parent in common, and that this parent was a 7 chromosome primary species, and contributed chromosome set *c* to *Ae cylindrica,* and also to vulgare wheats Whether *Ae cylindrica* or vulgare arose first there seems no evidence for determining However, the similarity in chromosome pairing seems to indicate that the time elapsing between the origin of the two was not very long It seems probable that the parent bearing chromosome set *c* might be in existence today, whether wheat- or Aegilops-like It is likewise possible that the parent bearing the *7* chromosome set *d* of *Ae cylindrica* may be in existence

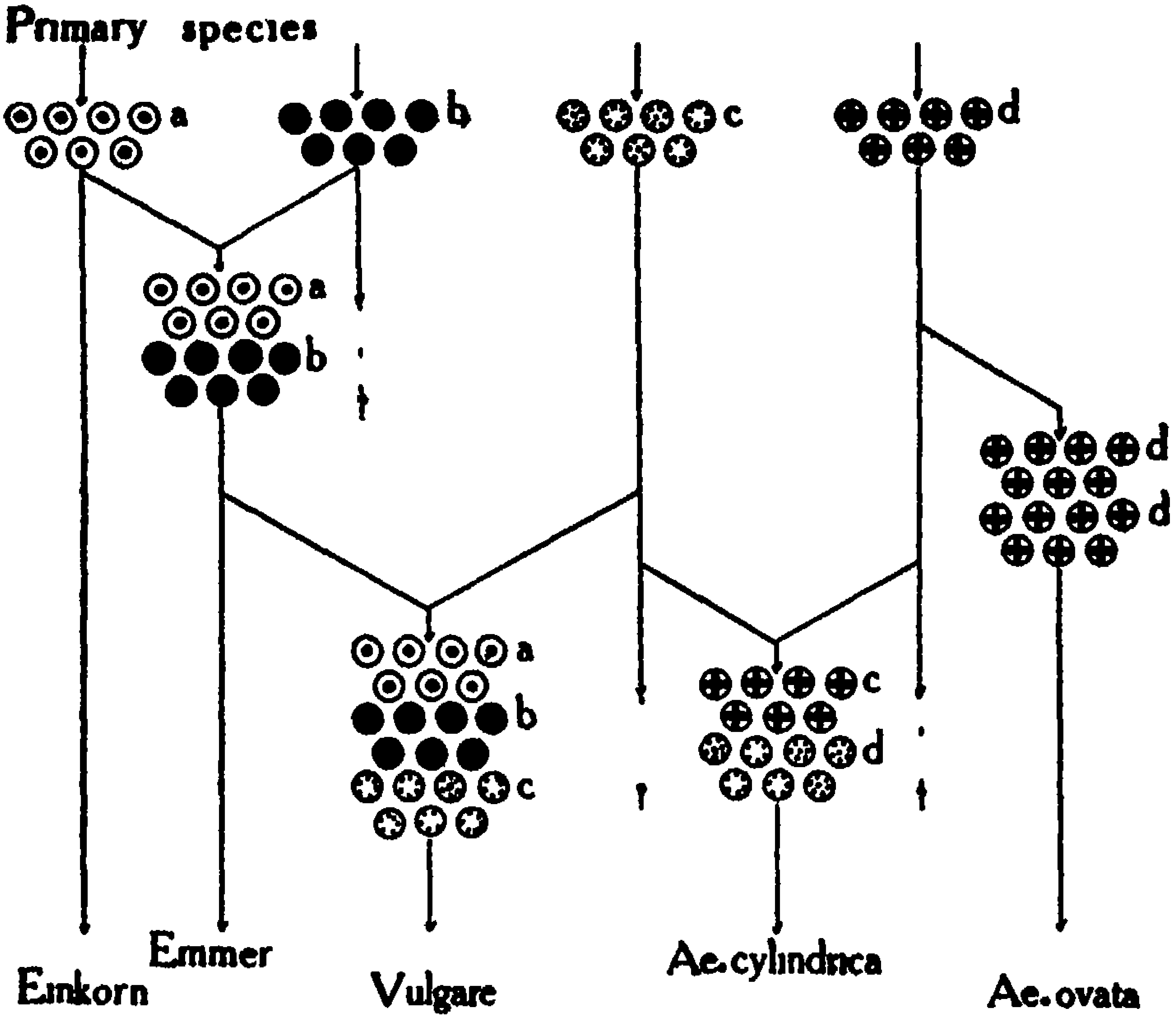


Fig 27 Diagram illustrating hypothetical relationships in wheat and Aegilops The vulgare group is assumed to comprise descendents of a hybrid, of comparatively recent origin, between an emmer a b and a primary species c the emmer group the descendents of a hybrid of comparatively ancient origin between two primary species a and b the einkorn group the descendents of the primary species a Aegilops cylindrica is a hybrid of comparatively recent origin and has one parent namely, primary species c, in common with vulgare wheat and one parent primary species d, in common with Ae ovata Ae ovata shows some indications of being a true tetraploid, in which case it must be the tetraploid form of the primary species d.

Jenkins (1929) in discussing the cytological results in the cross *Aegilops speltoides* x *T turgidum,* states as follows " at least one species of *Aegilops* has one set of 7 chromosomes which mate with those of *T turgidum* This set must therefore be either *A* or *B* and not *C* Accordingly the situation is not so simple as is indicated by the theory

"It will not solve the problem to suppose that in some species of *Aegilops,* including *A speltoides* used in this work, there is a chromosome set (*A* or *B*) corresponding to one of those in emmers, and that in other species, including *A cylindrica* used by other investigators there is a set corresponding to the *C* set of *vulgare* The single set in *A speltoides* must be the *C* set since it carries most of the characters which distinguish *vulgare* from the emmer wheats These characters (present in *A speltoides*) are (1) long hairs on the ridges of the leaves and none between, (2) thin-walled hollow culms, (3) greater width on the 1-ranked side than on the 2-ranked side of the ear, (4) rounded back of the empty glume, (5) no prominent keel, (6) broad apex of glume, (7) spreading habit of growth like 'winter' wheat

"Accordingly on the basis of their behavior in crosses with *T turgidum* the chromosomes of *A speltoides* must be *A* or *B,* while on the basis of the genes which they carry they must be *C* It is scarcely conceivable that all these genes would arise independently in two groups of *Aegilops* species"

Though *Ae speltoides* carries most of the characters which distinguish vulgare from the emmer wheats, table 1 presented by Jenkins, seems to indicate that this Aegilops species in the cross with an emmer has failed to produce a vulgare wheat comprising all the characters enumerated above

From a phylogenetic point of view the composite groups, emmer and vulgare, must each be considered as an entirety, that is, the varying offspring of each dates back possibly to a single cross (allowing for possible back-crosses) Sapehin in discussing his phylogenetic investigations in emmer and vulgare wheat states "The data of systematics (the works of Percival (7), Flaksberger (8), Vavilov (11), Barulina (12), Orlov (10) have shown that there is not one single character in which all biotypes of *durum* differ from all biotypes of *vulgare* Among *durum,* as among *vulgare,* biotypes may be found with an equal degree of markedness of the one or the other character (compactness of the ear, character of the keel, solidity of the straw, pubescence of the leaves, etc) Thus, in comparing ***durum*** and ***vulgare*** we find not one particular specific feature with which to characterize these species ***Durum,*** or correspondingly the emmer group, and ***vulgare,*** or correspondingly the ***vulgare group,*** differ only by combinations of many characters of the ear, every separate feature may be found in the one or the other combination of the ear without changing the character of the whole combination"

If the assumptions as to chromosome homology are correct, the vulgare wheats have resulted from a rather recent cross, yet the independent variations in the respective homologues have already resulted in a large complex of types of vulgare wheats Some of these may possibly be due to back-crossing to either of the parents or other types which had likewise arisen by variations in homologues It follows as a corrollary that the direct parents of the vulgare cross are represented today by a progeny, not of facsimiles of the original cross, but of somewhat modified forms It is probably not possible through hybridization of the descendents of primary species to duplicate any of the vulgare wheats in existence today

The question arises as to whether all the 21-chromosome (gametic) wheats have descended from only one hybridization The writer in comparing crosses with *T spelta* and *T vulgare* as the respective 21-chromosome parents has felt that *T spelta* and *T vulgare* differ somewhat in chromosome constitution Huskins (1930) states that he has observed chromosome irregularity in the meiosis of the *T spelta* x *T vulgare* cross The present more or less fragmentary observations must, however be reinforced by more abundant cytological data before a suggestion can be proposed in this connection

10 ***Emmer wheats are of ancient origin, descending from a hybrid between two 7-chromosome primary species whose mutual chromosome homology had become nil*** The einkorn wheats are probably descendents of the parent which contributed the 7-chromosome set designated as *a* As compared with emmer-vulgare and with *Ae cylindrica*-vulgare, einkorn-emmer shows considerable weakening in chromosome affinity and hence conjugation The average number of bivalents per cell is between 5 and 6, instead of 7, as should be expected if the hybrid were of comparatively recent origin The number of the closed type averages only a little higher than the open type The total number fluctuates

In *T* ***monococcum*** x *T* ***spelta*** and *T* ***vulgare*** x *T* ***monococcum*** with 0-5 bivalents (Table 3) the exaggerated failure in pairing is perhaps due to a disturbing influence of the larger number of chromosomes in the vulgare, affecting an already weakened chromosome affinity

It is, no doubt, futile at this time to attempt to suggest the identity of the parent which contributed the 7 chromosome set *b* It should probably be noted at this point, however, that Jenkins (1928) found in *T turgidum* var *buccale* x *Ae speltoides* bivalents approximating 7 in number The greater prevalence, apparently, of the open type indicates possibly a relationship of more ancient origin than in case of einkorn and emmer in spite of the fact that the number of bivalents approximates rather closely the latter crosses

11 *Ae ovata suggests in some respects true tetraploidy with two 7-chromosome sets d+ d* *Ae cylindrica* x *Ae ovata* indicates a triploid condition as to some of the chromosomes Two trisomes per cell, or almost seven times the maximum in any of the other hybrids, are observed in this cross Bivalents approximate the number 5, and univalents the number 7 In all Aegilops crosses studied cytologically, *Ae ovata* enters as one parent, hence it is not possible to state whether the unusual meiotic behavior in the 14 + 14 Aegilops hybrids is due to the chromosome complex of *Ae ovata* or is typical of all these tetraploid Aegilops hybrids

If *Ae ovata* is tetraploid it should form tetravalents at meiosis rather than bivalents Yet, the experimentally produced *Solanum* tetraploids described by Jorgensen form either bivalents or tetravalents Jorgensen suggests in this connection "It is true that some difficulty is caused by the cytological behaviour of the tetraploids A few (*Datura*) have a regular formation of tetrasomes at meiosis The others (*Primula sinensis*, the Oenotheras the Solanums, etc) have a normal gemini formation, but even here the four homologous chromosomes assort at random The segregation ratios found in heterozygous Daturas (Blakeslee) have proved this definitely They differ regularly from the usual Mendelian ones But as differentiation of the chromosomes by 'genomorphosis' proceeds the pairing will probably become selective, and the plants turn from the tetragenomatic condition into the digenomatic "

It is true that *Ae ovata* gives rise to no more bivalents when crossed with vulgare than when *Ae triuncialis* is used as the Aegilops parent, neither does it give rise to more bivalents than *Ae cylin-*

drica in crosses with emmers These facts seem to preclude autosyndesis Yet *Ae ovata* (Table 10) in a cross with vulgare gives rise to an average of 0 2 bivalents per cell, with emmer 0 7, and with einkorn 2 3 A large number of foreign chromosomes may serve as a hindrance to autosyndesis It is, however, premature to attempt any suggestions concerning the inter-relation of Aegilops species, as so little has as yet been learned about the cytology and genetics in this genus

12 *Chromosome conjugation is only one method of approach to the study of phylogeny* This article has dealt almost exclusively with chromosome conjugation with the full understanding that it is only one method, and not an infallible method, of approach to the complex problem of species formation in wheats and related plants Taxonomic and morphological studies, especially in Aegilops, studies of chromosome morphology as undertaken by Kagawa (1927, 1929 a,c), more extensive cytologic and genetic data concerning wheat and Aegilops hybrids, including the later generations, will no doubt, not only reveal new facts, but also point out errors in our present theories concerning the relationship in these cereal groups

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THE JAPANESE EXCLUSION BILL OF 1924

(An Historical Sketch)

EARL H PRITCHARD

In the spring of 1924 the anti-Japanese forces of the Pacific Coast, by a union with the anti-immigrant forces of the East and Middle West, succeeded in inserting a clause into the general immigration bill which in effect excluded Japanese immigrants from the United States The exclusion of the Nipponese marked the culmination of a long series of attacks upon Japanese immigration, the causes of which need not be mentioned here[1] The purpose of this paper is simply to trace the development of the particular exclusion bill which became law in 1924, and to note the various forces which influenced it from its first introduction to its final passage

The elemental ideas and phrases which constituted the exclusion sections had already been in existence for some time before 1924 For example, the idea of excepting from the general operation of the bill "officials, teachers, students, merchants, or travelers for pleasure or curiosity" dates back at least to the Chinese exclusion law of 1888[2] The convenient phrase, "alien ineligible to citizenship," was formulated in idea, if not in words, in the California Alien Law of 1913,[3] and was definitely used as a basis of discrimination in the Louisiana Alien Land Law of 1921[4] Finally, the idea of establishing certain classes not subject to the main immigration laws was more definitely formulated in the immigration bill of 1921 by the inclusion of the phrase, "aliens from countries immigration from which is regulated in accordance with treaties or agreements relating solely to immigration"[5]

A study of the immigration bills and committee reports upon them introduced into Congress during the year 1921 will show that the idea of Japanese exclusion did not very seriously occupy the minds of most congressmen,[6] furthermore, the immigration bill of that year passed Congress without dissent upon the clause especially excepting from the quotas, "aliens from countries immigration from which is regulated in accordance with treaties or agreements relating solely to immigration"[7] Apparently Congress was not yet vitally interested in Japanese exclusion

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[1] For a discussion of the Japanese immigration problem consult the facts and figures relating to Japanese immigration given in the Annual Reports of the Commissioner General of Immigration See also Raymond Leslie Buell Japanese Immigration (Boston, 1924) Roy L. Garis Immigration Restriction (New York 1927), Chap X, K K Kawakami The Real Japanese Question (Chicago, 1917), H A Millis Japanese Problem in the United States (New York 1915)

[2] K S Inui, The Unsolved Problem of the Pacific, p 358 See text of law

[3] Ibid., p 425 for text of the law

[4] Ibid., p 455 for text of the law

[5] U S. Statutes at Large, V 42, Part 1 Chap 8 p 5.

The force, however, which was to change the attitude of leaders in the House Committee on Immigration from a passive policy toward the Japanese to a militantly exclusive one was already at work This was the Japanese Exclusion League which had the support of other adherents of the exclusion policy The work of this group and its allies, linked with various investigations held by the Congressional Committees on Immigration, served, in the course of a few years, to mobilize public opinion both in and out of Congress in favor of exclusion

Historically, the exclusion clause of 1924 must date from April 4, 1921, when the Japanese Exclusion League of California, representing officially such organizations as the American Legion, War Veterans, Native Sons and Native Daughters of the Golden West, State Federation of Women's Clubs, State Federation of Labor, and with the approval of the Los Angeles County Anti-Asiatic Association, and the Japanese Exclusion League of Washington, was able to introduce into the California Senate a joint resolution calling for the

> Absolute exclusion for the future of all Japanese immigration not only male but female, and not only laborers, skilled and unskilled, but 'farmers' and the men of small trades and professions, as recommended by Theodore Roosevelt
>
> Permission for temporary residence only for tourists, students, artists, commercial men, teachers, etc.[8]

This resolution was eventually endorsed by the Senate and Assembly and copies of it were sent to the President, to the Secretary of State, and to each member of the California delegation at Washington[9] It reached Congress at a time when the quota bill for that year was in Conference and had no appreciable effect upon it, but it marked the beginning of a movement which culminated in Japanese exclusion [20]

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[6] Congressional Record, V 61 April 18 1921, House Report No 4, 67 Cong., 1st sess , Senate Report, No 117 67 Cong , 1st sess For two exceptions to this see Congressional Record, V 61, pp 182 and 520

[7] U S Statutes at Large, V 42 Part 1 Chap 8 p 5 see also Congressional Record, V 61 pp 495, 967, 1426 28, and 1592 This clause exempted Japanese from the action of the quotas

[8] California Senate Journal, 44th sess , April 4, 1921, p 1040 For text, see Congressional Record, V 61 pp 182 and 520

[9] California Senate Journal, 44th sess 1921, pp 1255 1845 1899

The Exclusion League followed the California resolution with a brief prepared by V S McClatchy, editor of the *Sacramento Bee* and secretary of the League It was a highly sensational document purporting to show the dangers from Japanese immigrants and pointing out why they should be excluded It was presented to the Secretary of State with the endorsement of the entire California delegation in Congress [21] On July 27, 1921, Senator Johnson of California introduced it into the records of the Senate with these words, "The brief is pertinent to a pending matter of very great consequence to the West and to the Nation too"[22]

During the summer and fall of 1921 the campaign against the Japanese continued to grow, and when Congress met, the question of immigration in general came up again, but this time a demand for Japanese exclusion also made its appearance in the Capitol Definite action upon Japanese exclusion was postponed until after the passage and approval, on May 11, 1922, of the joint resolution extending the quota bill of 1921 to June 30, 1924 [23] On June 26, Mr Johnson, chairman of the House Committee on Immigration, introduced H R 12169,[24] and on June 27 Mr Raker introduced H R 12193 [25]

Relative to his bill Judge Raker said in a speech on June 29,

> One of the vital and important provisions of this bill (H R 12193) is that which relates to ineligible aliens, which reads as follows
>
> > 'That no alien ineligible to citizenship under the laws of the United States shall be admitted to the United States'
>
> The bill also provides for the elimination and abrogation of what is known as the "Gentlemen's Agreement"[26]
>
> This bill was the first ever introduced in Congress carrying the provision that 'no alien ineligible to citizenship should be admitted to the United States'[27]

Mr Raker, not Mr Johnson, was the author of the first bill to exclude "aliens ineligible to citizenship," and during these early stages he seems to have been the leader in the House for Japanese exclusion

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[20] Congressional Record, V 61, May 7, 1921, p 1146

[21] Senate Document, No 55, 67 Cong 1st sess

[22] Congressional Record, V 61 July 27 1921, p 4382

[23] Ibid., V 62, June 29, 1922 p 9689

[24] Ibid., V 62, June 26, 1922 p 9489

[25] Ibid., V 62, June 27 1922, p 9540

[26] Ibid., V 62, June 29 1922, p 9689

[27] Ibid., V 65, May 15, 1924, p. 8689

These bills apparently were introduced not with the idea of passage during that session of Congress but rather to act as advance agents for bills to be introduced in 1923[28] On June 30 1922, Mr Johnson introduced a new immigration bill, which apparently satisfied Mr Raker, and which was to serve as the basis for the summer's investigation and the model for future thinking on immigration[29]

The Congress which met in the fall of 1922 was slow to take up definite consideration of the immigration question It would appear that both Houses were holding back, neither willing, until better informed, to take a definite step[30] It was also evident that opinion in the House had swung far more toward exclusion than had opinion in the Senate[31] On February 5, 1923, the Senate, showing its desire to avoid the issue, passed a bill to enable certain political refugees from the Near East to enter the United States[32] The House was goaded into action by this move Mr Johnson, on February 9, introduced a bill to restrict immigration, and on February 10, Mr Miller (of Washington) introduced a bill to exclude "aliens ineligible to citizenship"[33] These two bills the House Committee on Immigration and Naturalization combined into one which it submitted to the House on February 15, in the form of an amendment to the Senate bill[34]

The immigration bill, found in *House Report* No 1621 for 1922-23, was very comprehensive, and served as a model for those bills introduced into the first session of the 68th Congress in 1923-24[35]

In section 3, the above mentioned measure defined *an immigrant* as any alien departing from a place outside of the United States destined for the United States, except (1) government officials, their families and servants, (2) aliens visiting the United States temporarily as tourists or for business or pleasure, (3) aliens in continuous transit through the United States, (4) aliens lawfully admitted who in transit from one part of the United States to another go through foreign contiguous territory, (5) and bona fide seamen It also, in section 4, defined ***non quota immigrants*** as (c) immigrants who have previously been lawfully admitted to the United States and who are returning from a temporary trip abroad, (e) ministers or professors, and (h) students over sixteen years of age

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[28] Ibid., V 62 June 29 1922 p 9689

[29] Ibid. V 62 June 30 1922 p 9879

[30] According to the Congressional Record, V 64 there were prior to Feb 9 1923 ten bills introduced into Congress relating to immigration but only one of them was ever reported back by the committees See pp 24, 207 502, 783 843 1212 1273 1447, 2043, and 2291

[31] Ibid., V 64, March 3 1923 pp 5435 38

[32] Ibid., Feb 5 1923 pp 3034 36

[33] Ibid., Feb 9 and 10 1923, pp 3380 and 3444

[34] Ibid., Feb 15 1923 p 3735 (See House Report, 1621)

[35] Ibid., March 2, 1923 pp 5181 82—Johnson's report on the work of the Committee on Immigration and Naturalization

It then proceeded to say

> An *immigrant not eligible to citizenship* shall not be admitted to the United States unless such immigrant is admissible as a non-quota immigrant under the provisions of subdivision (c) (e) or (h) of sec 4, or (2) is the wife or unmarried minor child of an immigrant admissible under subdivision (e) and is accompanying or following to join him[26]

In connection with this it must be explained that the United States nationalization laws denied citizenship to all persons except free whites and persons of African nativity or of African descent[27] The provision thus worked effectively to exclude all Asiatics, Japanese included It will be noted that no provision was made for guarding the treaty rights of Asiatic peoples

This bill never came to a vote, although some interest in Asiatic exclusion was manifested by a memorial from the Oregon Legislature which arrived on February 19[28] Mr Johnson, however, in a speech supporting the bill, gave notice that during the next session a second measure embodying these principles would be introduced[29]

During the recess between the last session of the 67th Congress and the first meeting of the 68th, which had been elected in the fall of 1922 partly, at least, upon the issue of immigration restriction or freedom, the propaganda to convince the country and the new Congress of the necessity of Japanese exclusion continued The California Legislature early in May adopted two memorials to be sent to the Congress of the United States One demanded the exclusion of aliens ineligible to citizenship, and the other asked that the Constitution of the United States be so amended as to make all persons born in the United States of parents ineligible to citizenship also ineligible to citizenship[30]

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[26] House Report, No 1621, 67 Cong 4th sess pp 2 and 5

[27] Inui op cit, pp 416 19 see also decision of the Supreme Court in the case of Takao Ozawa vs United States 1922, in Buell op cit., pp 345 46

[28] Oregon Senate and House Journal, 1923, pp 60 61 Congressional Record, V 64 Feb 19 1923 pp 3931 32

[29] As explained by Mr Johnson fear that filibustering would prevent passage of the bill and so preclude the relief measures for the Near Eastern refugees kept it from coming to a vote See Congressional Record, V 64 March 2 1923 pp 5131 32

[30] California, Senate Journal, 45th sess, 1923 pp 755 56 1527 2089

When Congress opened in December, 1923, the matter of immigration was given immediate consideration Several bills were introduced into the House to regulate immigration and out of these Mr Johnson drafted H R 6540 which was introduced on February 1, 1924[21] On February 9, 1924, the Committee on Immigration reported the bill back to the House (H Report 176)[22] The majority report was favorable Its main features corresponded exactly with the bill introduced during the previous session Its only change in purport was to raise the age of students exempted from exclusion from sixteen to eighteen years, and to lower the age for the exemption of unmarried children of professors and preachers from twenty-one (minors) to eighteen[23] It also failed to protect treaty rights

On February 8, Secretary Hughes addressed a reply to Mr Johnson's earlier letter of inquiry relative to bill 6540 He objected to the bill for two reasons First, it violated existing treaties of commerce and navigation, especially that with Japan To remedy this he suggested that an additional class of people be added to those defined as non-immigrants, to include "an alien entitled to enter the United States under the provision of a treaty" Second, he objected to the clause excluding aliens ineligible to citizenship, because of its unjust discrimination against the Japanese The clause, he thought, was not only unnecessary, but would not accomplish its ostensible purpose as well as would further executive agreement with Japan He asked that the clause be struck out, and the Japanese placed upon a quota basis[24] This protest arrived too late to influence House Report 176

As a result of the protest and certain technical considerations, Mr Johnson, on March 17, introduced H R 7995 which was ultimately enacted into statute[25] This bill was reported back from the Committee (H R 350) on March 24[26] The Committee after due consideration had decided not to eliminate the exclusion clause It had, however, added the following subdivision to section 3 defining non-immigrants, who would escape the exclusion proviso, as "aliens entitled to enter the United States solely to carry on trade under and in pursuance of the provisions of a present existing treaty of commerce and navigation."[57] This provision guarded the treaty rights of aliens, but carefully limited these rights to the strict letter of the Japanese treaty of 1911.[58] In this form the bill adhered to the letter of existing treaties, but without any respect for the sensibilities of the Japanese, baldly excluded them as a group.

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[21] House Journal, 68 Cong 1st sess 1923 24 pp 19, 21, 31 74, 85, 94, 113, 114, 131, 133 138 159 178 194 and 216

[22] Ibid., p 289

[23] House Report, No 176, 68 Cong, 1st sess, 1923 24.

[24] International Conciliation, No 211 Diplomatic Relations between the United States and Japan 1908 1924 ' pp 176 81

[25] House Journal, 68 Cong, 1st sess 1923 1924, p 348

[26] House Report, No 350, 68 Cong, 1st sess, p 2 and House Journal, 68 Cong., 1st sess., p 366

In the meantime the Senate, with less zeal but with equal effectiveness, had taken up the problem of immigration. Several bills were introduced to limit it, and on February 20, 1924, Mr. Reed, of Pennsylvania, introduced Senate Bill 2576 which was to serve as the contribution of the upper house to the immigration legislation of the year.[59] This bill had the advantage of Secretary Hughes' suggestion that it should not contain an exclusion proviso. It also proposed to include in the non-immigrant classes, "an alien entitled to enter the United States under the provision of a treaty."[60] In this form the measure eliminated both points to which Mr. Hughes had objected in House Bill 6540.

The bill now went to the Committee on Immigration, of which Senator Colt, an opponent of exclusion, was chairman. On March 11, Secretary Hughes addressed a letter to the Senator reiterating his suggestions of February 8 to Mr. Johnson, and urging him to "avoid the affront of the enactment of any exclusion provision."[61] Upon the basis of this recommendation and other considerations of expediency, the Senate Committee, on March 27, reported the bill back with a further concession.[62] This was done despite special demands for exclusion which were introduced into the Senate on March 13 from ex-Senator Phelan, of California,[63] and on March 25 from the Japanese Exclusion League and its supporters, the American Federation of Labor, the American Legion, the National Grange, and from the Long Beach (California) Committee Regarding Japanese Immigration.[64]

The concession which the Committee proposed was an amendment to be added to the treaty exception provision, above mentioned, to make it read, "an alien entitled to enter the United States under the provision of a treaty, or *an agreement relating solely to immigration*."[65]

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[57] House Report, No. 350, 68 Cong., 1st sess., pp. 1, 9.

[58] William M. Malloy, Treaties and Conventions of the U. S., V. 3, pp. 2712-13.

[59] Senate Journal, 68 Cong., 1st sess., pp. 6, 78, 71, 104, 136, and 161.

[60] Congressional Record, V. 65, April 2, pp. 5409-10 and 5415.

[61] Letter of Hughes to Senator Colt, March 11, 1924, in Buell, op. cit., p. 357.

[62] Congressional Record, V. 65, April 2, 1924, p. 5415, and March 27, 1924, pp. 5055-56.

[63] Ibid., March 13, 1924, p. 4078.

[64] Ibid., March 25, 1924, pp. 4929-35.

[65] Ibid., April 2, 1924, p. 5415.

This would have recognized the "Gentlemen's Agreement" and would have avoided all possible discrimination against the Japanese On March 27, 1924, the two Houses, therefore, stood in direct opposition in regard to the Japanese exclusion question

On April 7, Mr Hughes addressed letters to Mr Johnson and Mr Frothingham, both of the House of Representatives, advising against the passage of the exclusion provision[46] The next day Mr Free, addressing the House, spoke of the menace of the "Yellow Peril," and bewailed the fact that the Japanese were acquiring control of all the land and industries in California and that their birth rate was dangerously high He also charged the "Gentlemen's Agreement" with allowing thousands to come in, and demanded that it be abolished and the Japanese excluded[47]

On April 12, the bill came up for a vote in the House, and the exclusion clauses as reported by the Committee were passed by an overwhelming majority[48] Mr Burton alone voiced a protest because he felt it unwise to offend a friendly nation in order to exclude the forty-six immigrants[49] which would enter under the quotas He further believed that upon the basis of Japan's attitude the question might be successfully settled by diplomacy

If the Senate Committee on Immigration was not disposed to exclude the Japanese, these sentiments were not shared by all the Senators On April 2, when Senate Bill 2576 came up for first discussion[50] Senator Shortridge, of California, was ready with two amendments One proposal was to add a new paragraph excluding aliens ineligible for citizenship with certain exceptions, while the second was to limit the treaty exemption clause by amending it to read, "an alien entitled to enter the United States solely to carry on trade under and in pursuance of the provisions of a present existing treaty of commerce and navigation"[51] These amendments would have brought the bill into almost exact conformity with that of the House

By April 14 when the bill came up for consideration a great change in attitude had come over the Senate[52] This was due to a sentence in Ambassador Hanihara's letter of April 10 to Secretary Hughes in which he discussed the "Gentlemen's Agreement." In protesting against the exclusion clause found in the House bill, he referred to "the *grave consequences* which the enactment of the measure retaining that particular provision would inevitably bring upon the otherwise happy and mutually advantageous relations between our two countries."[53] This letter was introduced into the Senate on April 11.[54] This phrase, which taken in its true setting was perfectly harmless, was viewed as a "veiled threat" by certain members of the Senate. It, together with an earlier appeal to the American people against discriminatory legislation, issued by Japan's Foreign Minister through the Associated Press on February 7,[55] was considered an impertinent attempt on the part of Japan to influence domestic legislation, and caused many Senators to vote for exclusion as a protest against such interference.[56]

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[46] Ibid, pp 5840 and 5882

[47] Ibid, April 8 1924 pp 5924 26

[48] Ibid., April 12 1924 p 6258

[49] Ibid., pp 6249-51 The number 46 was given by Mr Burton but seems to be inaccurate

[50] Ibid., April 2 1924, p 5898

[51] Ibid, pp 5410-11

[52] Ibid., April 14, 1924 p 6302

Senator Reed who had formerly been opposed to Japanese exclusion by statute now declared himself forced "on account of that veiled threat, to vote in favor of the exclusion, and against the committee amendment."[57] Senator King suggested the possibility of executive abrogation of the agreement as a means to avoid "brutal and rude" action.[58] Senator Sterling alone pleaded against such narrow-minded legislation and asked that, "If we are going to exclude Japanese immigrants, let us exclude them because it is wholesome."[59]

The opinion of the Senate had, however, turned against Japan, and the Committee amendment to the treaty-exemption clause, "or an agreement relating solely to immigration," was defeated by a large majority.[60] Senator Reed immediately proposed to make the clause read, "an alien entitled to enter the United States solely to carry on trade under and in pursuance of the provisions of a present existing treaty of commerce and navigation." The amendment was passed.[61] Two days later the Senate in Committee of the Whole, passed an exclusion provision similar to that of the House. On April 18 the Senate further amended the bill so that it would take effect at once,[62] and changed the age at which students would be admitted from eighteen to fifteen[63] The bill as amended was agreed upon and sent to the House with a request for a Conference[64]

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[53] Hanihara to Hughes April 10, 1924 in Buell op cit., pp 358 62 Italic is the writer's insertion

[54] Congressional Record, V 65 April 11 1924 pp 6073 74

[55] Ibid., Feb 25 1924 p 3084

[56] Ibid., April 14 1924 p 6305 for statement of Senator Lodge

[57] Ibid., p. 6305

[58] Ibid., p. 6306

[59] Ibid., p 6308

[60] Ibid., pp 6314-15

[61] Ibid., pp 6315 16

[62] Ibid., April 16 and 18, 1924 pp 6460 and 6644

The House and Senate bills which were now to be united in the Conference were practically identical in so far as the exclusion clauses were concerned During the Conference, and prior to May 1, the President attempted to secure a modification of the bill He suggested that the exclusion clause should not take effect until March 1, 1926, with the proviso,

> That the provisions of this paragraph shall not apply to the nationals of those countries with which the United States, after the enactment of this act, shall have entered into treaties by and with the advice and consent of the Senate for the restriction of immigration[65]

The Conference refused to do this, and proceeded, on May 6, to hold its final meeting, in which the only recorded change was the adoption of the age of fifteen as the lower limit for admittance of students[66] So nearly complete was the work of the Conference that it issued a statement to the press and determined to meet the 7th to consummate the agreement The next morning President Coolidge, upon the request of Mr Johnson, invited the Republican members to the White House and suggested that the following be added to the exclusion clause

> That this subdivision shall not take effect as to exclusion until March 1, 1925, before which time the President is requested to negotiate with the Japanese Government in relation to the abrogation of the present arrangement on this subject

The Republican majority of the Conference accepted this suggestion, and it was added to the Conference Report[67]

This report was submitted to the House on May 9 Furious debate arose, and telegrams poured in from Washington and California demanding that the amendment be rejected[68] The House and Senate were afraid that the amendment would in some way leave room for a treaty regulating immigration, or lead to other complications by setting a precedent, so the bill was recommitted to the Conference with instructions that the amendment be struck out[69] On May 15 the Conference Report was returned with the objectionable feature removed, and it passed the House by a vote of 308 for, 62 against, and 63 not voting [70]

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[63] Senate Journal, 68 Cong 1st sess , 1923 24 p 281

[64] Ibid., pp 270 and 281

[65] Congressional Record, V 65 May 9 1924 p 8235

[66] Ibid., pp 8231 35 House Journal, 68 Cong 1st sess , p 505

[67] Congressional Record, V 65 May 9 1924 pp 8231 2 8235 36.

[68] Ibid., pp 8233 34 and 8237 38

[69] Ibid., p 8249 For details of debates in House see pp 8218 49 Discussion in Senate see May 8 1924, pp 8085 87

As has been indicated the immigration bill of 1924 was the result of a union of anti-Japanese and anti-immigration ideas, the latter being of interest to a far larger group of people than the former An analysis of the petitions and memorials presented to Congress shows that the East was interested primarily in limiting European immigration [71] The West was willing to cooperate with the East, but its main interest was in the exclusion of the Japanese [72] The Pacific Coast thus took advantage of the interest of the East in general immigration restriction to secure, during the excitement, a bill excluding Asiatics Had the question of exclusion been determined entirely upon its own merits, it seems unlikely that the anti-Japanese party could have mustered so much support

The most noticeable thing about the entire course of the argument upon the exclusion bill was that it constantly avoided the real issue Most people were willing to concede that the exclusion of Japanese immigration, or at least a very severe restriction of it, was necessary and desirable The real question at issue, then, was *how* it should be done The leaders of the anti-Japanese group, however, almost completely ignored this fact, and centered their energy upon pointing out the economic, social, political, and cultural dangers resulting from immigration People became so aroused over these arguments that they could not see that friendly cooperation with Japan in restriction, plus the quotas, which put a maximum of 146,[73] would be a far more effective limitation than the exclusion bill which aroused dislike in Japan and terminated Japanese cooperation

The State Department and the President alone remained calm and looked at the problem in its true light They, however, accomplished nothing for their trouble, while the diplomatic protests of Japan served as a goad to the resolute Senate The main objections to Japanese immigration which were advanced, such as non-assimilation, economic competition, vice, high birth rate, and the like, although good arguments if the country had been threatened with a deluge of Orientals, really missed the point at issue The best argument which the friends of exclusion had was that the Japanese could not become citizens and, therefore, little good would come through increasing the number in the United States The contention that the matter must be settled now, for all time, also had some foundation On the other side the argument was simply that it was bad diplomacy to exclude by statute, and so discriminate against the nationals of a friendly power, when the same end might be better accomplished by friendly agreement

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[70] Ibid., May 15, 1924 p 8652

[71] Based upon a study of the petitions delivered to the Senate in 1923 24, found in Senate Journal, 68 Cong 1st sess

[72] There is in the Senate Journal for the 68 Cong 1st sess but one petition from an exclusively Eastern organization demanding exclusion This was from the United American Mechanics, of Newton N H, and was introduced on April 24 (See p 297) On the other hand, there are four petitions representing Eastern churches the Association to Abolish War of Boston, and the Women s Christian Temperance Union of Lisbon Ohio, protesting against exclusion (pp 312 and 368) The greater part of the active support outside of Congress to Japanese exclusion apparently came from the West

[73] See Buell, op cit., p 361

On May 15, 1924, the final Conference Report was passed upon in the House and was sent to the Senate[74] The following day the Senate agreed to the report,[75] and on May 19 it was sent to the President[76] On the 26th President Coolidge signed the document and it became the law of the land[77] The President gave his consent to the exclusion features with regret, as was shown by his statement upon signing the bill[78]

As finally passed and approved, the measure excluded from the United States all persons ineligible to citizenship except

> (1) a government official his family attendants, servants, and employees, (2) an alien visiting the United States temporarily as a tourist or temporarily for business or pleasure, (3) an alien in continuous transit through the United States, (4) an alien lawfully admitted to the United States who later goes in transit from one part of the United States to another through foreign contiguous territory, (5) a bona fide seaman serving as such on a vessel arriving at a port of the United States and seeking to enter temporarily the United States solely in the pursuit of his calling as a seamen, (6) an alien entitled to enter the United States solely to carry on trade under and in pursuance of the provisions of a present existing treaty of commerce and navigation, (7) an immigrant previously lawfully admitted to the United States, who is returning from a temporary visit abroad, (8) professors and preachers, (9) the wives or unmarried children under eighteen years of age of the above professors and preachers, and (10) bona fide students at least fifteen years old[79]

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[74] House Journal, 68 Cong 1st sess p 584

[75] Ibid., p 540

[76] Ibid p 558

[77] Ibid, p 616

[78] See Buell op cit. p 371

[79] U S Statutes at Large (1923 25) V 43 Part I Chap 190 pp 154-162

Into the Japanese protest and the exchange of diplomatic notes which followed the passage of this bill we need not go Suffice it to say that clear-headed thinking on the part of the diplomats of both countries helped to smooth over difficulties which might easily have led to severe complications As time has passed, agitation has died down and friendly relations have been established between the two great peoples, but the Japanese are still waiting for the time when America will do an about-face and right what they consider an unjustifiable wrong

GENETIC CHARACTERS IN RELATION TO CHROMOSOME NUMBERS IN A WHEAT SPECIES CROSS *

F J STEVENSON

Species crosses have been used only to a limited extent as a means of obtaining improved varieties of wheat and only a very few results of practical value have been secured Marquillo, a spring wheat variety recently distributed to the farmers of the State of Minnesota, was obtained from a cross of Marquis *(Triticum vulgare)* and Iumillo *(T durum)* It has twenty-one pairs of chromosomes, is about equal to Marquis in milling and baking qualities and has at least two genetic factors for stem rust resistance which it inherited from its durum parent Hope, a variety of wheat immune to many of the physiologic forms of stem rust, was obtained from a cross of Yaroslav Emmer *(T dicoccum)* and Marquis *(T vulgare)* It is a vulgare variety with the stem rust resistance of the Emmer parent

In the present investigation, the relationships between chromosome numbers, characters of keel, collar, stem cavity, glume shape, reaction to stem rust and reaction to leaf rust were studied in segregates of a pentaploid hybrid Velvet Don *(T durum)* x Quality *(T vulgare)* The F_1 had twenty-one chromosomes in the metaphase of the first division, fourteen bivalents and seven univalents The F_1 plants had a durum type of keel and collar, and intermediate condition for stem cavity, glume shape, and beards, but pubescence and red seed color similar to the durum parent They were susceptible to stem rust like the vulgare parent They set seed to the extent of about five per cent

Association between the chromosome number of each species and the typical characters of the same is apparent in the F_2 and F_3, but recombinations of the characters of both species are relatively frequent Relatively homozygous, fertile F_3 segregates with the vulgare chromosome number, keel, collar, stem cavity and glume shape combined with the stem rust resistance of the durum have been obtained One fertile vulgare-like F_3 segregate had the leaf rust resistance of the durum

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* This is a summary of a thesis presented at the State College of Washington in partial fulfillment of the requirements for the degree of Doctor of Philosophy

Durum-like plants with fourteen chromosome pairs were found which were as susceptible to stem rust as the vulgare parent All the plants of one F_3 line had fourteen pairs of chromosomes and durum-like characters but with an intermediate type of resistance to leaf rust, although they varied somewhat in this respect One F_3 plant with fourteen pairs of chromosomes was completely sterile, and three others almost sterile, giving only a few shriveled seeds

The relative frequency with which recombinations of the characters of the two species occurred is evidence that a cross of this kind can be used to advantage in building a new variety with the desirable characteristics of both species

MORPHOLOGICAL STUDY OF BULB AND FLOWERS OF CAMASSIA QUAMASH (PURSH) GREENE *

ANNE MACLAY LEFFINGWELL

INTRODUCTION

The following investigation was carried on in an effort to determine the development of the bulb and flower parts of *Camassia quamash* (Pursh) Greene

The common blue camas of the Palouse region of Washington was first described by Frederick Pursh (1814) from material collected by Lewis and Clark in Montana, and named by him *Phalangium quamash* This same plant was again described by Edward Lee Greene (1895) as *Camassia quamash* (Pursh) Greene, which is valid under the International Rules It is the *Quamasia quamash* (Pursh) Coville, of Piper's Flora of Washington (1906), which is valid under the American Code

Piper and Beattie (1914) list but one species, *Quamasia quamash,* for the area covered by the Flora of Southeastern Washington and Adjacent Idaho The general range of this plant extends from British Columbia to Montana, and southward to Utah and California

The usual habitat is low, so-called camas prairie In this the basaltic soil is very soft and wet in the spring but dry and hard in the summer months In the neighborhood of Pullman the camas is usually found along the Palouse River bed

Members of the genus *Camassia* have been cultivated for more than one hundred years, the eastern form having been taken to England by Nuttall about 1810 Bailey (1914 and 1924) states that *C quamash* has been grown very successfully in the eastern states

BULB DEVELOPMENT

The seeds are angular, hard, black and shining, about the size of those of the common onion In actual measurement they average about 4 by 2 5 mm Germination tests were made shortly after the seed became mature, with negative results Later tests were made in February

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* This article includes the findings listed in a thesis presented at the State College of Washington in partial fulfillment of the requirements for the degree Master of Science in Botany

Contribution No 28 from the Botany Department of The State College of Washington

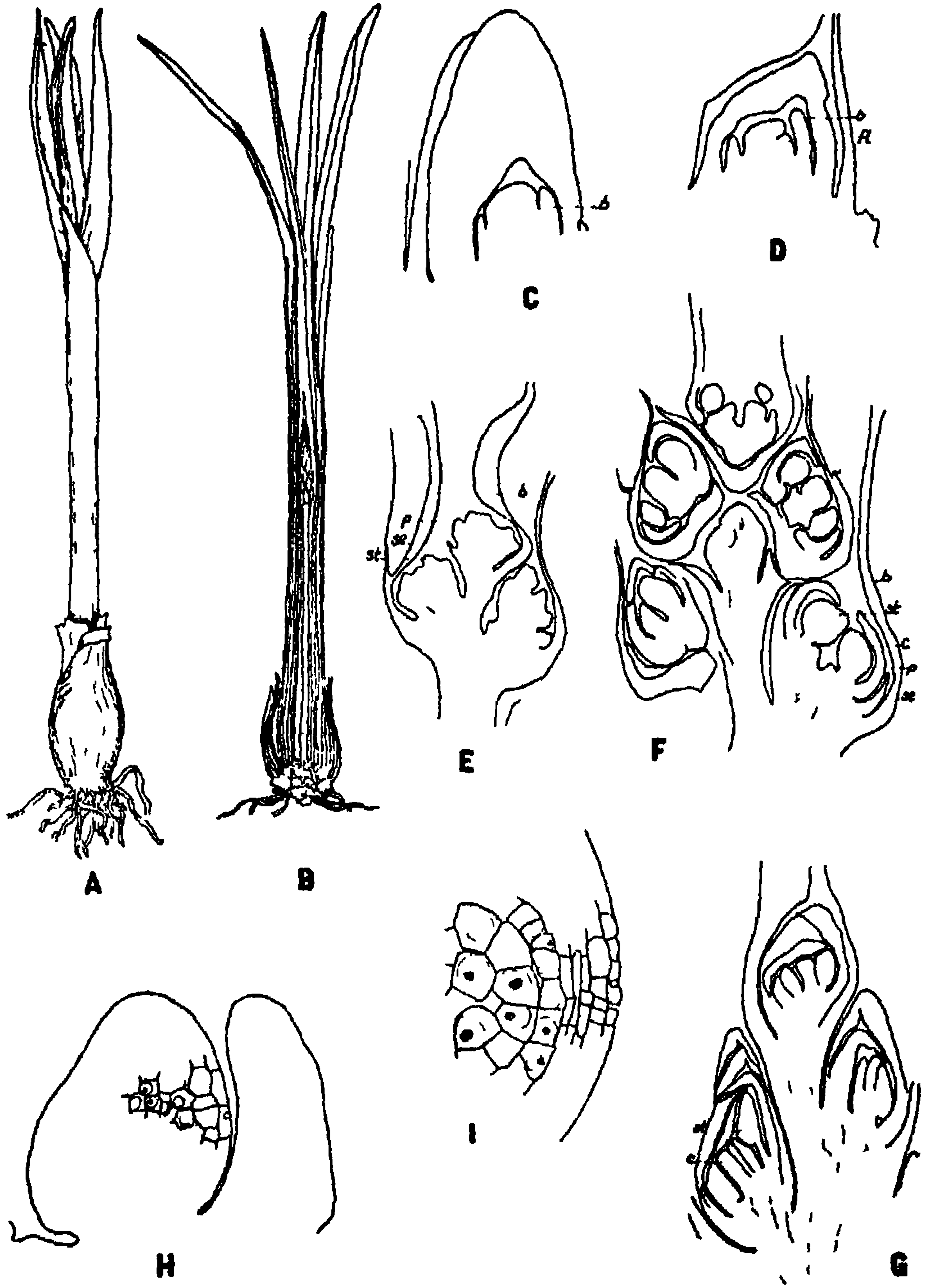

Fig 1 **Camassia quamash** Floral development A normal plant early in growing season, (Collected April 15 1927) X 2 5 B longitudinal section of A C bud showing primordium of flower cluster X 20. D single flower(fl) differentiated bract (b) X 20b E cluster showing sepal (se), petal (p) stamen (st) X 20 F beginning of carpel development (c) X 20 G, carpels elongated but not yet united X, 20 H section through stamen showing sporogenous tissue X 250 I cross section of stameen showing pollen mother-cells, uninucleate tapetum X 250

and March One seed germinated after thirty days, a few after forty and a larger percentage after sixty days Bailey (1914) found that four years is required to produce a blooming bulb The same bulb will produce flowers for an indefinite period of years

A bulb taken early in February or March, shows the following characteristic structure from the outer portion to the center (Fig 1, B)

1 It is covered by a thin, deep brown layer of almost completely disintegrated tissue

2 There is a region of several (5-7) white, fleshy leaf bases or scale leaves

3 The base of last season's flower stalk is surrounded by the scales in 2

4 Surrounded by the scales of 2 are several small developing scales These will produce a new mass of fleshy scales as growth continues

5 A well-developed flower spike is present with florets which will mature within the next few weeks

6 A central mass of meristematic tissue forms a terminal bud This will develop next season's shoot

All of the above mentioned parts are attached to a flat basal callus from which the roots grow

Growth begins with the development of new leaves from the meristematic mass After the usual number of these leaves is developed, the meristematic region continues to elongate and forms the primordium of the flowers In the development of the flower cluster the bracts appear first In their axils the single florets develop The floral cycles form in acropetal succession (Fig 1, C, D)

THE PERIANTH

The two circles of the perianth segments develop at practically the same time, very soon after the general meristematic areas appear in the axils of the much elongated bract They grow rapidly and form an enclosing envelope, before the sporogenous tissue in the anther develops or the carpels begin to differentiate (Fig 1, E)

THE STAMEN

The stamen first appears as a conical mass of tissue in the axil of the perianth segment, which differentiates only a little earlier than the stamen primordium It is foliar in origin as shown by material collected March 24, 1927, in which the flower spike is still enclosed within the

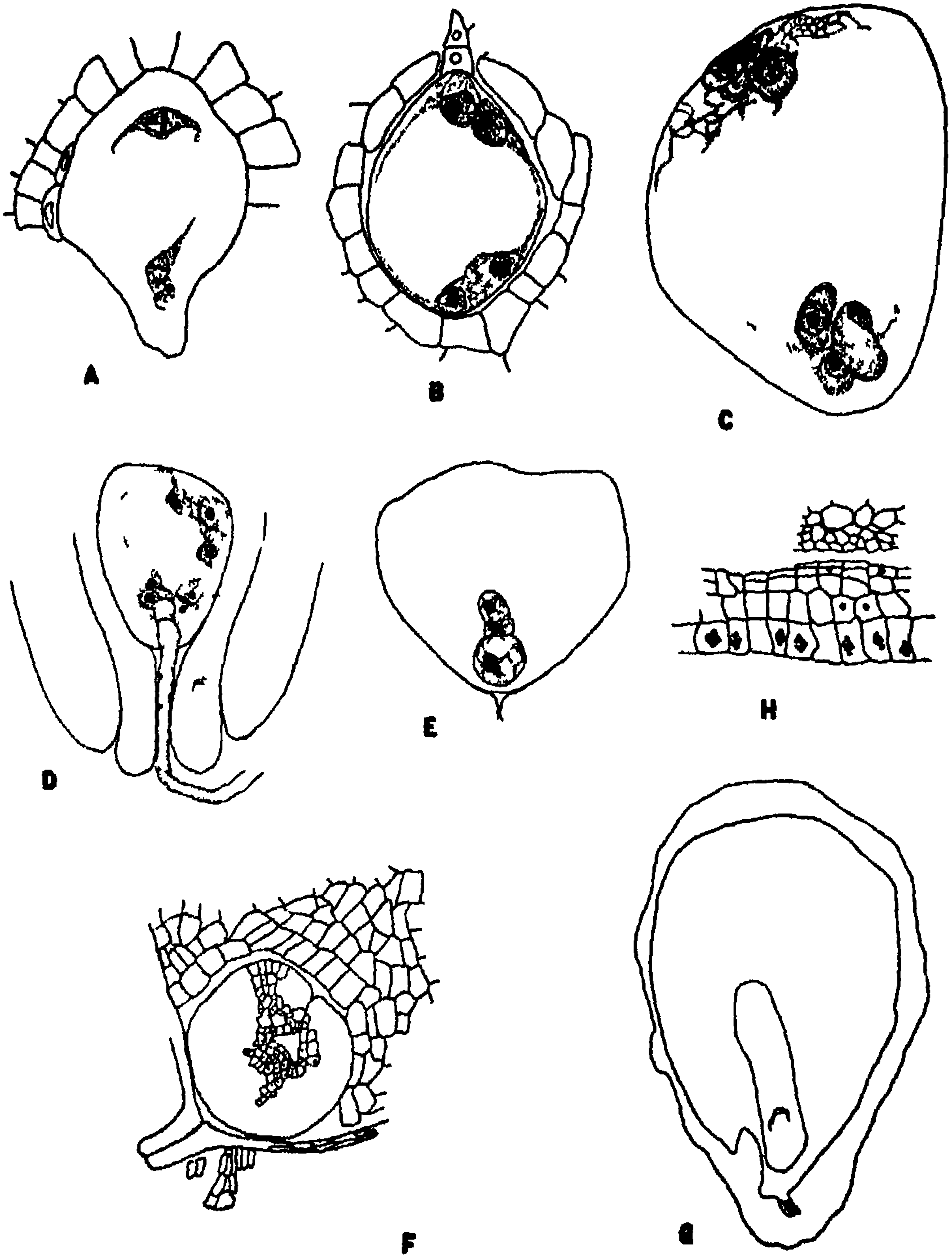

Fig 2 Section of stamen pollen mother cells binucleate tapetum (t) X 260 B, divisison of pollen mother cell X 450 C tetrad division X 450 D E sections through pistil showing infolding and union of carpels X 45 F ovules developing X 45 G, section of ovule—megaspore mother cell X 700 H, primary parietal cell and primary sporogenous cell—Integuments forming X 650 I, mature egg cell—Integuments developed X 650 J, Embryo sac X 650 K Binucleate egg sac X 650

bulb scales At this stage the carpels have just begun development and may be observed as three small outgrowths from the terminal meristematic region (Fig 1, F)

Sporogenous tissue is formed in the autumn of the year prior to blooming, as shown by material collected October 19, 1927 The pollen mother-cell stage is the normal winter condition (Fig 1, H, I) The mother cells have a characteristic hyaline envelope, thickened on two sides and evident up to the early telophase in the tetrad division (Fig 2, B, C)

Maturation of the pollen grains requires a relatively short time The first activity at the beginning of the growing season is the division of the mother cells In material collected April 5, 1927 in which the flower spike had emerged only a few millimeters from the bulb scales, synapsis and daughter cells and tetrads were found In the formation of microspores, both successive and simultaneous types of division are found in the same anther

The pollen grains are normally mature before the other flower parts are fully developed Material collected April 26, 1927, shows them in the binucleate condition

From three to five parietal layers are differentiated outside the sporogenous tissue by the periclinal division The middle layers, two to three in number, of narrow elongated cells finally become crushed and disintegrated The inner layer becomes the tapetum Its development is the same as in other genera of*Liliaceae* Early in the growing season it may be observed as a compact layer of uninucleate cells, only a little smaller than the pollen mother-cells (Fig 1, I, material killed April 5, 1927) Material collected about ten days later shows the tapetalcells as binucleate, and the pollen mother-cells in synapsis The tapetal cells at this time are elongated, the two nuclei almost filling the cavity (Fig 2, A) The tapetal layer disintegrates about the time of the pollen development through the tetrad stage This condition is shown in material examined from collections made April 26, in which the grains are mature

The mechanism of dehiscence requires more study The endothecium is not strongly developed Dehiscence takes place by means of a longitudinal fissure, within a few hours after the flower opens

The filament does not elongate greatly until the perianth segments are nearly mature Elongation then takes place rapidly and ceases at the end of a few hours

THE PISTIL

The carpels are the last organs to develop They appear after the perianth segments and stamens are well advanced They are first seen as three protuberances surrounding the axis of the individual flower shoot (Fig 1, F) These elongate rapidly without uniting The edges gradually infold and coalesce at the lines of contact, forming the outer ovary wall and the three-chambered ovary normally found (Fig 2, D, E, F)

The style elongates slowly In material examined, in which the ovary is completely formed and shows the megaspore mother-cell stage in the ovules, the style has begun to extend only very slightly Here the separate carpel tips are seen as individual projections When these unite there is left a very narrow canal in the center which remains open throughout the life of the flower The style elongates rapidly just before the opening of the flower and continues to grow for a very brief period after the perianth segments unfold The average length of the style is about 15 mm

Before the infolded walls, forming the septa of the ovary, have completely united, small irregularities appear on their inner edges These develop rapidly by division of the cells just beneath the epidermis, until a very marked protuberance is formed By the middle or latter part of April the mother cell begins formation Material collected April 21, 1927, shows the single enlarged mother cell just beneath the epidermal layer (Fig 2, G) Soon this cell cuts off a parietal cell toward the periphery The megaspore mother cell begins to elongate immediately Free nuclear division takes place at once Material collected May 6, and May 10, 1927, shows active division in several stages in the ovules of the same ovary The development of the eight-nucleate embryo sac is normal (Fig 3, A, B, C)

At the time of the development of the embryo-sac the integuments are forming When the megaspore mother-cell first appears there is no trace of the integuments (Fig 2, G) Then a slight protuberance is formed on either side from which will develop the inner integuments (Fig 2, H) A few days later the second integuments are clearly differentiated At this time the inner pair has grown nearly together and inclosed the nucllus (Fig 2, I)

At maturity the ovary normally is inflated and three-angled The placenta is large and fleshy The ovules arise anatropously Only about two-thirds of them mature

Although the usual number of carpels in *Camassia quamash* is there, some material was found having five distinct carpels Each of these produced the normal two ranks of ovules

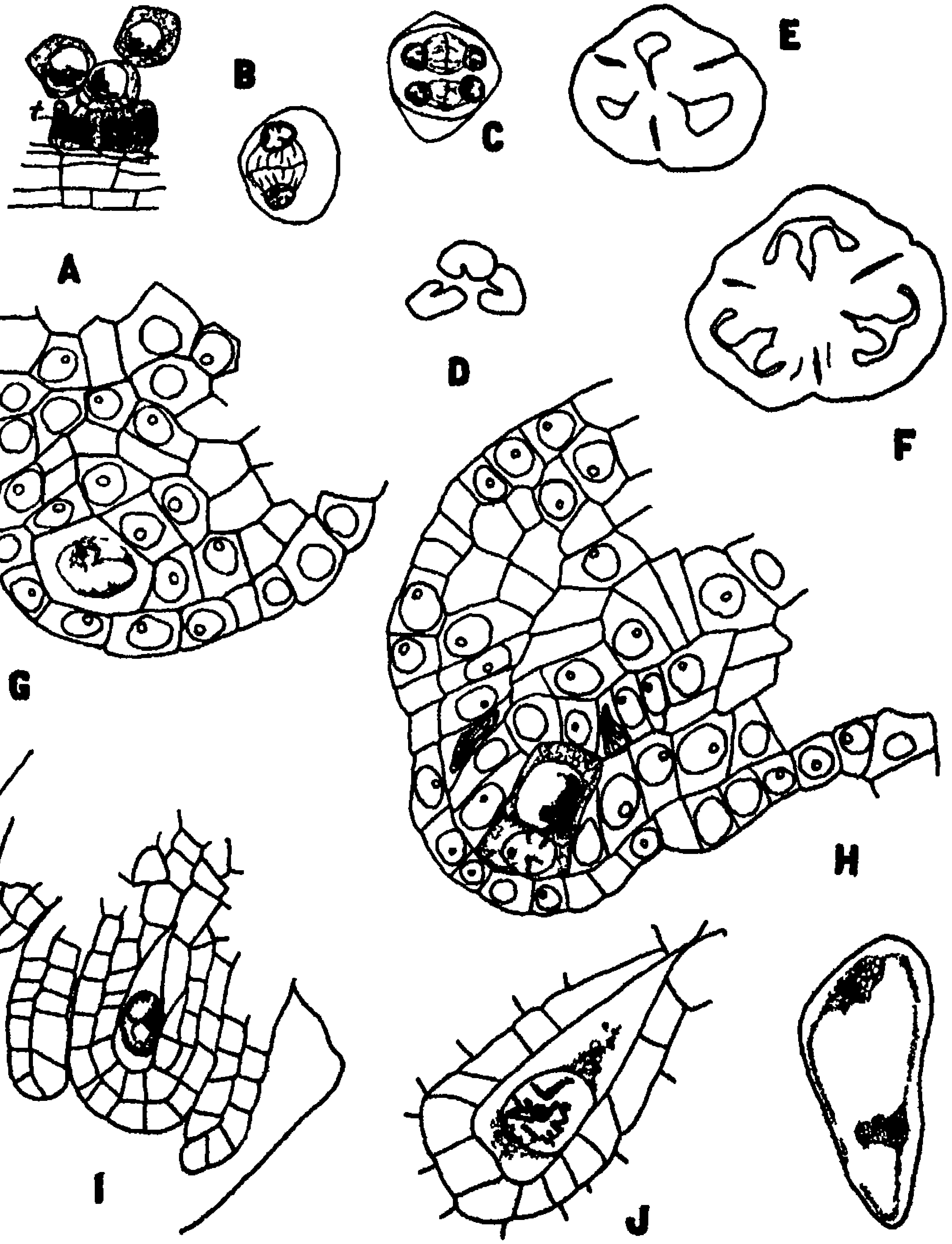

Fig 3 Embryo development. A, B, C, formation of eight-nucleate embryo-sac. X 470 D pollen tube entering egg sac. X 170 E, F G, development of embryo E. X 170 F X 75, G X 25 H, detail of development of endosperm X 75

FERTILIZATION AND EMBRYOGENY

In an effort to determine the length of time for fertilization to take place, flowers were hand-pollinated and pistils then killed at intervals of from two to eighty-six hours Longitudinal sections were made of the styles and both cross and longitudinal sections made of the ovaries

In material pollinated from six to fifteen hours, the pollen tubes were found penetrating the style and a few entering the ovary chamber Evidently several hours elapse from the time of their entry into the ovary and subsequent union with the nuclei of the embryo sac The pollen tube was actually entering the micropyle at the end of the forty-two hours (Fig 3, D)

The opening in the style forms a continuous passage into the ovary The canal is only a little larger than the width of the pollen grain In several cases pollen grains were found near the base of the style and within the ovary itself It was at first believed that these might be the functional grains in fertilization However, examination did not reveal a single one germinating, while tubes from those germinating on the stigma were plentiful, in some cases almost filling the hollow style

The embryo development is normal for the lily family (Fig 3, E, F, G)

ENDOSPERM

The endosperm begins development in fifty to sixty hours after fertilization Then free nuclear division takes place, mostly around the fertilized egg When the embryo has reached about an eight-celled stage there are numerous free nuclei scattered through the embryo sac From this time on the endosperm develops rapidly until a layer several cells in thickness is formed about the periphery of the sac The cells of the innermost layer divide by periclinal division almost simultaneously, forming a complete new layer of tissue with each division (Fig 3, H) Then growth continues very slowly until the embryo is nearly mature The central cavity of the embryo sac remains filled with a thin, cytoplasmic material Before the maturity of the seed this cavity becomes filled with large thin-walled cells, which later become flinty in texture and a milky white in color

MATERIALS AND METHODS

In order to make detailed study of the development the following technique was used Collections were made at intervals of from twenty-four to forty-eight hours throughtout the growing season, beginning

March 24, 1927 and continuing through the dormant period in the autumn and through the spring of 1928

Three standard killing reagents were used, Chromo-acetic, Turtox, and Bouin's solution With Chromo-acetic, dilutions of 5 and 1% were used

Materials were sectioned from 12 to 15 microns in thickness, and stained with Fleming's triple stain, saffranin, gentian-violet, and orange G

SUMMARY

1 The bulb is composed of several fleshy scales attached to a disk-like basal callus and surrounded by an outer compressed, disintegrating layer The immature flower spike develops in the autumn of the season prior to blooming Spring growth begins with the development of new leaves from the terminal bud

2 The floral cycles develop in acropetal succession

3 The stamens begin formation about the same time as do the perianth segments The pollen mother-cell stage is the normal winter condition The mother-cells divide at the beginning of the growing season both successively and simultaneously Pollen grains mature early, before other flower parts are fully developed

4 The pistil is the last organ to develop The ovules appear before the complete union of the edges of the three foliar carpels The style elongates 12 to 15 mm and remains hollow in the center The development of the eight-nucleate embryo-sac is normal for *Liliacae*

5 Fertilization takes place about forty-two hours after pollination The embryo development is normal

6 The endosperm begins development in fifty to sixty hours after fertilization At maturity it is flinty milk-white tissue

ACKNOWLEDGMENT

The writer wishes to express grateful appreciation to members of the faculty of the Botany Department, Dr F L Pickett, Dr H C Aase, and Dr H St John, for assistance and advice in the completion of this work

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RESEARCH STUDIES
OF THE
STATE COLLEGE OF WASHINGTON

THE UPWARD MOVEMENT OF INORGANIC SOLUTES IN PLANTS - - - - - - - *Harry F Clements*

STUDIES IN LOCAL IMMUNITY - - - - - *L A Barnes*

NEW AND NOTEWORTHY NORTHWESTERN PLANTS - *Harold St John*

Pullman, Washington
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NOTE

Indexes for Volumes I and II of the Research Studies will be sent with Number 4 of Volume II

THE UPWARD MOVEMENT OF INORGANIC SOLUTES IN PLANTS*

HARRY F CLEMENTS

INTRODUCTION

Prior to the last decade, plant physiologists generally assumed that inorganic salts moved upward in plants with the water through the xylem, while the organic materials moved through the phloem At the beginning of the last ten-year period, two quite different views have been taken by certain schools One school, for example, asserts that the movement of both organic and inorganic solutes is in the xylem, while the other school declares that such movement takes place chiefly in the phloem That both of these views are entirely correct is impossible, that either of them is entirely wrong is improbable Since the knowledge of the movement of materials is of importance from the physiological as well as the horticultural point of view, it was thought advisable to pursue some studies of this phenomenon of translocation It is the object of this paper to present some data regarding the upward movement of inorganic solutes in certain plants

HISTORICAL

In 1920, Curtis began a series of experiments the object of which was to study the movement of solutes, particularly organic solutes, in plants Two papers in 1920 dealt with this phase (3-4) In 1923, in another paper, Curtis concluded that, "The data show that a ring distinctly hinders the movement of nitrogen and of ash constituents into the leaves above the ring, either when the ring is made in the spring before the leaves open and the new xylem is laid down, or when it is made in the summer after they have opened and the new xylem is partly or fully formed" (5) In 1925, another article appeared by the same author in which he states in conclusion, "It seems the solute movement, both upward and downward occurs chiefly through the phloem tissue" (6) In 1926, he adds this, "The evidence, though perhaps not conclusive, at least clearly indicates that upward movement of solutes occurs chiefly in the phloem" (7) Another paper, in 1929, carries the statement, "The evidence clearly indicates that living cells take an active part in both the upward

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* Contribution No 30 from the Botany Department of the State College of Washington

and downward solute translocation It also supports the hypothesis, suggested by ringing and xylem cutting experiments, the upward movement of solutes takes place chiefly through the phloem" (8) Thus, as the years passed, Curtis became more and more firmly convinced that mineral nutrients moved upward through the phloem

Dixon (9), during the same general period, was as firmly convinced that the chief movement of all solutes was taking place through the xylem He employed dyes in his experiments and found that if the top portion of a plant was removed and a dye brought in contact with the wound, the dye would move downward through the xylem That this movement was due to suction force existing in the xylem is perhaps demonstrated by the fact that this dye will not travel backward through the xylem if the plant were allowed to come to equilibrium in a water bath after its top is removed and before the dye is applied

Mason and Maskell (10) found that ringing a stem interrupts the downward transport of carbohydrates in a stem, and does not interrupt the downward movement of dye in the wood, thus demonstrating that the dye movement in Dixon's experiment and the actual movement of carbohydrate solutes are two fundamentally different processes Their results, together with those of Curtis, seem to show that at least the greater movement of organic solutes takes place through the phloem It still remains to be seen whether or not both carbohydrates and nutrient salts move in the same channel If these solutes used the same channel, a simultaneous movement in both directions would be necessary, since the general direction of carbohydrates is downward while that of the soil solutes is upward

METHODS

The chemical data to be subsequently presented were gathered during the year 1927 at the Michigan State College Experiment Station, East Lansing, Michigan The plants studied included *Vitis vinifera L ,* *Prunus americana, Rubus occidentalis, Rubus idaeus,* varitey *strigosus,* (Cuthbert), *Rubus neglectus,* (Columbian) The Plum was growing in a waste corner of the experimental field, and the grape was growing near it in a fence row The black raspberry and the red raspberry were growing in the experimental plots The general plan of the experiment was to select pairs of healthy canes of each of the above plants One of these canes was girdled[1], while the other one of the pair was removed for immediate analysis The following numbers of pairs were used Twenty-two pairs of one-year-old grape twigs, seven pairs of one-year-old plum twigs, one pair of black raspberry vegetative canes, ten pairs of Cuthbert raspberry canes, and five pairs of Columbian raspberry canes These girdles were made early in April just as the buds were well swollen No attempt was made to protect the wounded portions[1]

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[1] The cooperation of Dr C W Bennett in girdling the raspberries is gratefully acknowledged

Analyses were made to determine the total nitrogen and ash contents of the canes Weights of the materials were taken in both fresh and dry conditions Drying was effected in an oven heated to 90° C until the subsequent weights of the samples became constant The dried material was then ground up and preserved for analysis in tightly stoppered bottles The girdled canes and twigs were allowed to remain attached to their respective plants until a maximum development had apparently taken place, at which time they were removed at the point of the girdle, weighed, and dried quickly under the same conditions as the checks, then ground, and finally stored until the analyses were to be made

Since each of the grape and plum twigs which were removed as checks was too small to be used as an individual sample for analysis, the grape twigs as well as those of the plum were bunched and analyzed as single samples The individual check canes of the raspberries, as well as the girdled canes of the grape and the raspberries were used as single samples The girdled twigs of the plum were again grouped as a composite sample

TOTAL INORGANIC NITROGEN

Whenever the size of the sample allowed, duplicate 2-gram portions were used Those canes whose dry weight was insufficient for such duplicates were divided into two parts and analyzed The official Kjeldahl method was used without the modification for nitrate and nitrite nitrogen

ASH ANALYSIS

The ash content of the samples was determined wth 2-gram duplicates, although with some of the material smaller samples had to be used The ashing was accomplished in alundum crucibles after the plant material had been mixed with 15 cc of a glycerin-ethyl alcohol (1-2) mixture The material was ignited and thoroughly charred over a Bunsen flame, after which it was removed to a gas furnace for complete incineration

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[1] In this paper the word girdle will mean the removal of a band of bark one half inch wide around the stem as far in as the xylem

All analytical results are reported in percentages based on the dry material

ANATOMICAL STUDIES

The material used for anatomical studies was gathered from the horticultural plots of the State College of Washington near Pullman, Washington, with the exception of the peach material, which was obtained from a nearby farmer These collections were made in the fall of 1929 after the plants were dormant The materials selected were Cuthbert raspberry (vegetative canes), one-year-old peach twigs (*Prunus Persica*), one-, two-, and three-year-old apple twigs (*Pyrus Malus*), and one-year-old twigs of the grape This material was cut into pieces one-half inch long and pickled in formalin-alcohol (6 parts of formalin to 100 parts of 50 per cent ethyl alcohol) After having been thoroughly fixed, the material was dehydrated and finally imbedded in paraffin In order to soften the tissue to facilitate microtome sectioning, the paraffin blocks containing the material were soaked in water for approximately one month Paraffin sections were then obtained with little difficulty Sections were made from 10 to 12 microns in thickness This material was then placed on slides and stained with safranin and gentian-violet

RESULTS

The results of the ringing experiments are given in Tables I to V In every case, there has been a large increase in the amount of nitrogen and ash after the stems were girdled Taking as unity the nitrogen content of the checks, the girdled twigs of the grape at the end of their experimental period had increased from 1 7 to 220 times in their nitrogen content It is only fair to state that the grape samples 3, 4, 13, 19, and 20 may well have been barred from consideration since slugs had eaten a good portion of the young leaves early in the experiment These twigs never completely recovered The girdled twigs had from 27 3 to 90 5 times as much ash in them at the end of the season as the checks had at the time the girdles were made

Table 1

Data Gathered from Girdled and Ungirdled Grape Stems

	Green Weight	Dry Weight	Total Nitrogen	Total Nitrogen	Total Ash	Total Ash	Increase in Nitrogen	Increase in Ash
Sample Number	Grams	Grams	Per Cent Dry Matter	Grams	Per Cent Dry Matter	Grams		
Ungirdled canes (Average of 22)		899	1 76	0158	4 41	0396	1 00	1 00
Girdled cane 1	21 5	6 1	2 03	1238	4 35	2653	7 80	
″ ″ 2	14 0	3 5	1 87	0645			4 10	
″ ″ 3	10 5	3 2	1 42	0454			2 90	
″ ″ 4	14 0	4 2	1 11	0466			2 90	
″ ″ 5	90 0	28 0	1 34	3752			23 70	
″ ″ 6	172 0	59 6	2 54	1 4638	5 09	3 339	92 60	90 50
″ ″ 7	128 0	36 6	2 41	8831	5 03	1 8409	55 90	46 50
″ ″ 8	114 0	36 1	1 92	6931	5 42	1 9566	43 80	49 40
″ ″ 9	149 0	39 5	1 84	7266			45 90	
″ ″ 10	97 0	29 6	2 59	7666	4 92	1 4563	48 50	39 40
″ ″ 11	23 0	7 2	1 54	1109			7 02	
″ ″ 12	229 0	69 5	2 17	1 5081			95 40	
″ ″ 13	7 0	1 5	2 26	0341			2 10	
″ ″ 14	16 0	4 8	1 96	0941			5 90	
″ ″ 15	62 0	19 0	1 88	2572	5 70	1 0830	16 20	27 30
″ ″ 16	102 0	30 7	2 01	6171			39 00	
″ ″ 17	192 0	59 0	2 57	1 5166			96 00	
″ ″ 18	450 0	132 8	2 62	3 4790			220.20	
″ ″ 19	8 5	3 2	1 77	0566			3 50	
″ ″ 20	9 0	1 3	2 11	0273			1 70	
Average increase over checks							42 5	50 62

TABLE 2

Data gathered from Girdled and Ungirdled Plum Stems

	Dry Weight	Total Nitrogen	Total Nitrogen	Increase in Nitrogen
	Grams	Per Cent Dry Matter	Grams	
Ungirdled stems Average of seven	2 06	2 48	0510	1 0
Girdled stems Average of six	6 71	2 12	1412	2 7

The plum was not, apparently, a good selection for experimentation An average of six girdled twigs showed an increase in total nitrogen of 2 7 times that of the check The vascular anatomy of this plant accounts perhaps for this small increase, and will be discussed later The leaves of the girdled twigs rolled as though suffering from a lack of moisture That this perhaps was the cause for the rolling was shown when after a rainy day and night the leaves unrolled and presented horizontal surfaces to the sun

The black raspberry showed luxuriant growth in spite of the girdle It grew well and produced abundant foliage and after a time produced a number of lateral shoots which grew downward in an attempt to reach the ground and take root This was prevented by tying each branch as it grew The girdled cane assimilated 3 8 times as much nitrogen as the control plant analyzed at the time the first plant was girdled This cane increased in ash content 4 3 times

TABLE 3

Data Gathered from Girdled and Ungirdled Canes of Black Raspberry

	Green Weight	Dry Weight	Total Nitrogen	Total Nitrogen	Total Ash	Total Ash	Increase in Nitrogen	Increase in Ash
	Grams	Grams	Per Cent Dry Matter	Grams	Per Cent Dry Matter	Grams		
Ungirdled stem	32 0	13 2	2 05	2706	6 02	7826	1 0	1 0
Girdled stem	119 5	56 5	1 81	1 0230	5 98	3 3780	3 8	4 3

The girdled canes of the Cuthbert raspberry showed very large increases in both green and dry weight, and also in nitrogen and ash in comparison with the amounts of those substances at the time the girdles were made They grew well and produced an abundance of fruit (Fig 1)

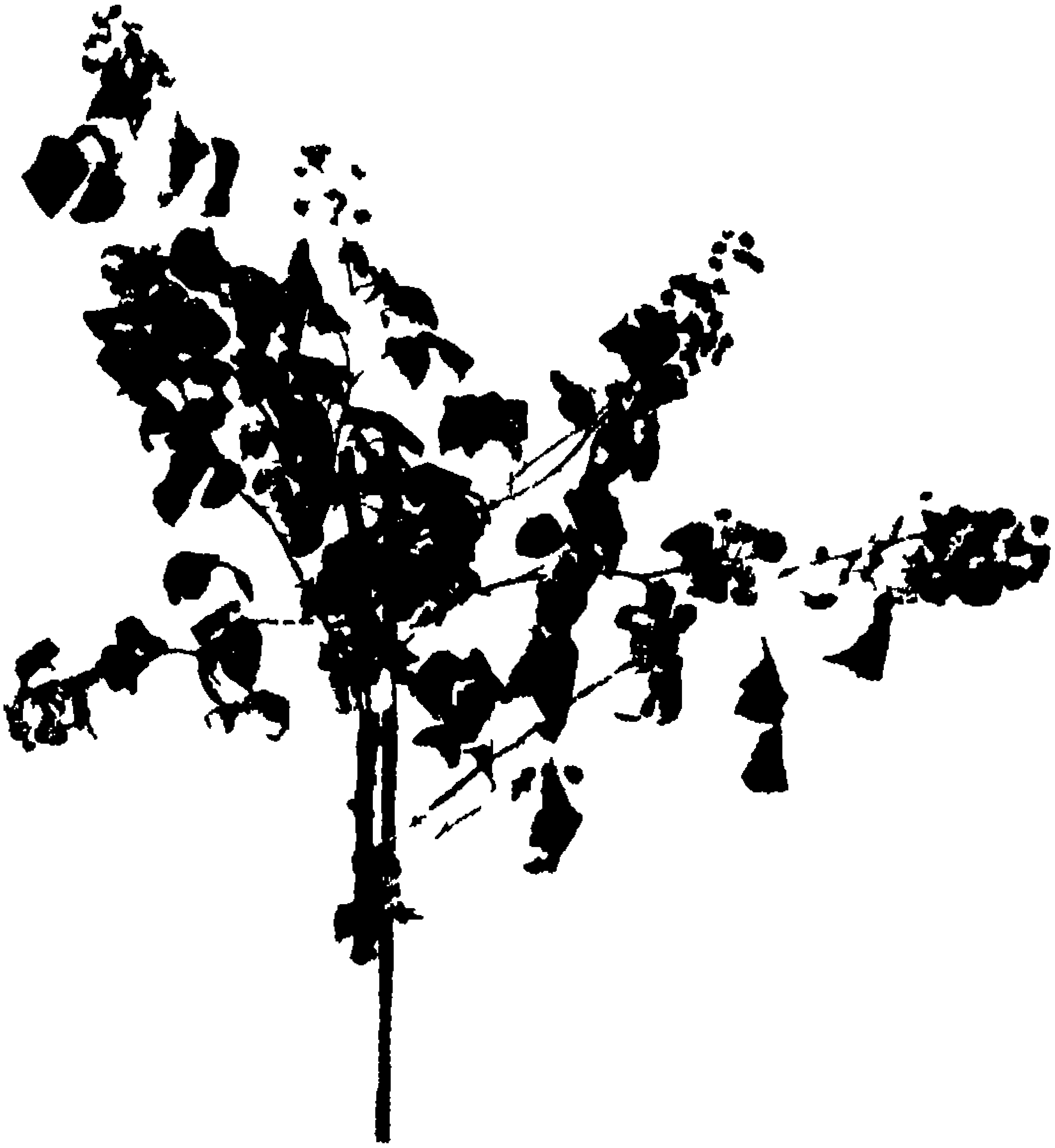

Fig. 1. A cane of the Cuthbert raspberry which had been girdled early in spring. It produced abundant fruit and foliage before it was removed from the plant at the point of girdling.

TABLE 4

Data Gathered from Girdled and Ungirdled Canes of the Cuthbert Raspberry

Sample Number		Green Weight	Dry Weight	Total Nitrogen	Total Nitrogen	Total Ash	Total Ash	Increase in Nitrogen	Increase in Ash
		Grams	Grams	Per Cent Dry Matter	Grams	Per Cent Dry Matter	Grams		
Ungirdled cane	1	12.2	5.32	1.04	0653				
" "	2	9.2	4.89	68	0333				
" "	3	16.6	5.42	1.12	0607				
" "	4	12.4	6.35	1.11	0705	3.65	.2317		
" "	5	11.5	5.25	1.19	0625				
" "	6	11.6	5.85	1.27	0743	2.78	1626		
" "	7	10.9	5.30	1.39	0737				
" "	8	12.6	6.22	84	0522	3.45	2146		
" "	9	10.6	5.22	85	0444				
" "	10	15.3	7.66	1.00	0766				
Average				949	0613	3.29	2029	1.00	1.00
Girdled cane	1	55.8	22.8	1.12	2547				
" "	2	101.5	37.0	1.59	4770	5.16	1.909		
" "	3	20.0	30.5	1.87	5703				
" "	4	56.0	20.2	1.42	2868				
" "	5	64.2	28.5	1.75	4988	4.93	1.405		
" "	6	26.5	13.2	1.04	1373				
" "	7	20.0	10.8	1.40	1512				
" "	8	55.7	21.0	1.59	3839	4.56	9576		
" "	9	76.7	30.0	1.65	4950				
Average				1.49	3561	4.88	1.423	5.80	7.01

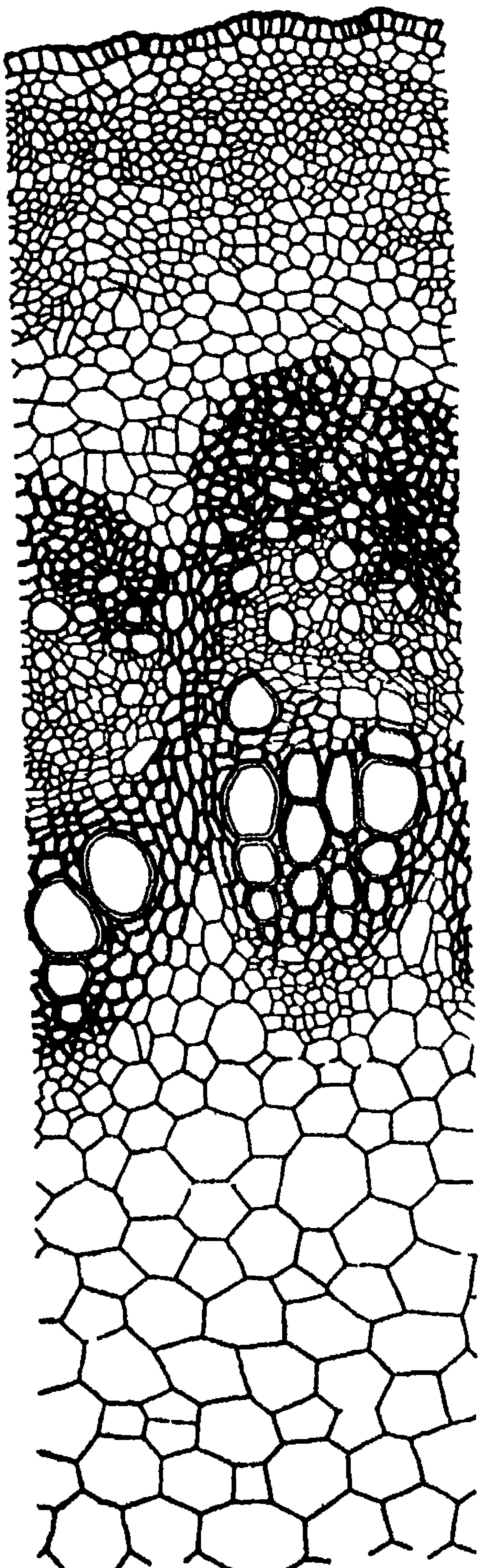

Fig 2 Tranverse section of a one year old grape stem showing the large thin wall tracheae closely bordering the cambium (x150)

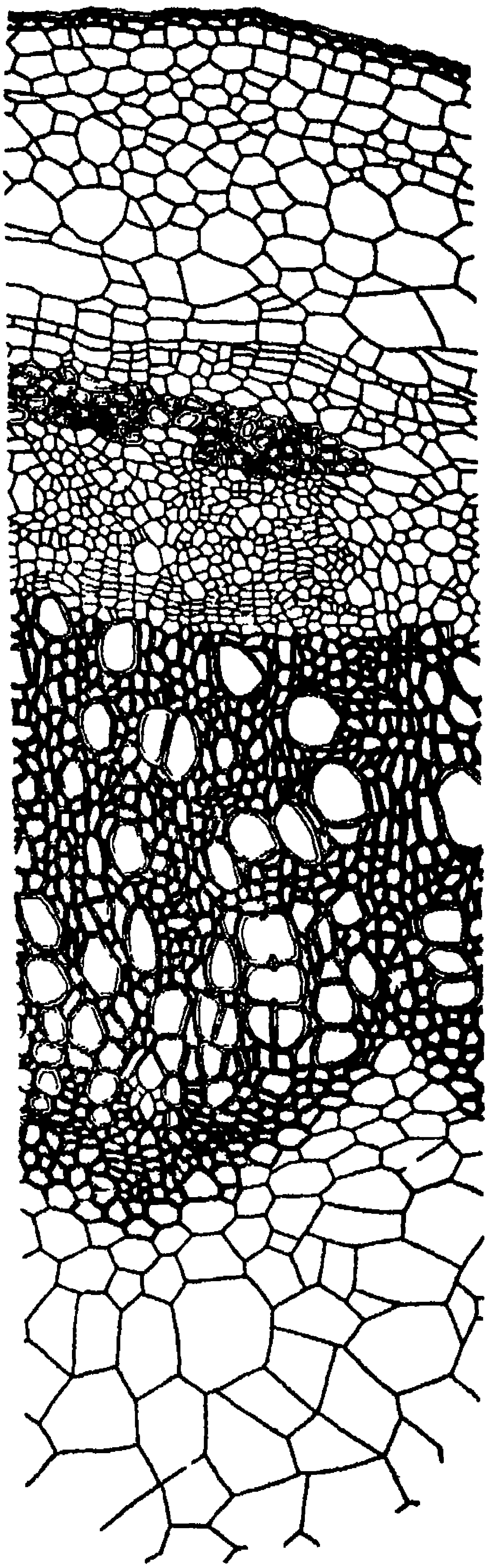

Fig 3 Transverse section of a vegetative cane of the Cuthbert raspberry showing a tendency toward ring porosity but with a number of vessels closely bordering the cambium (x150)

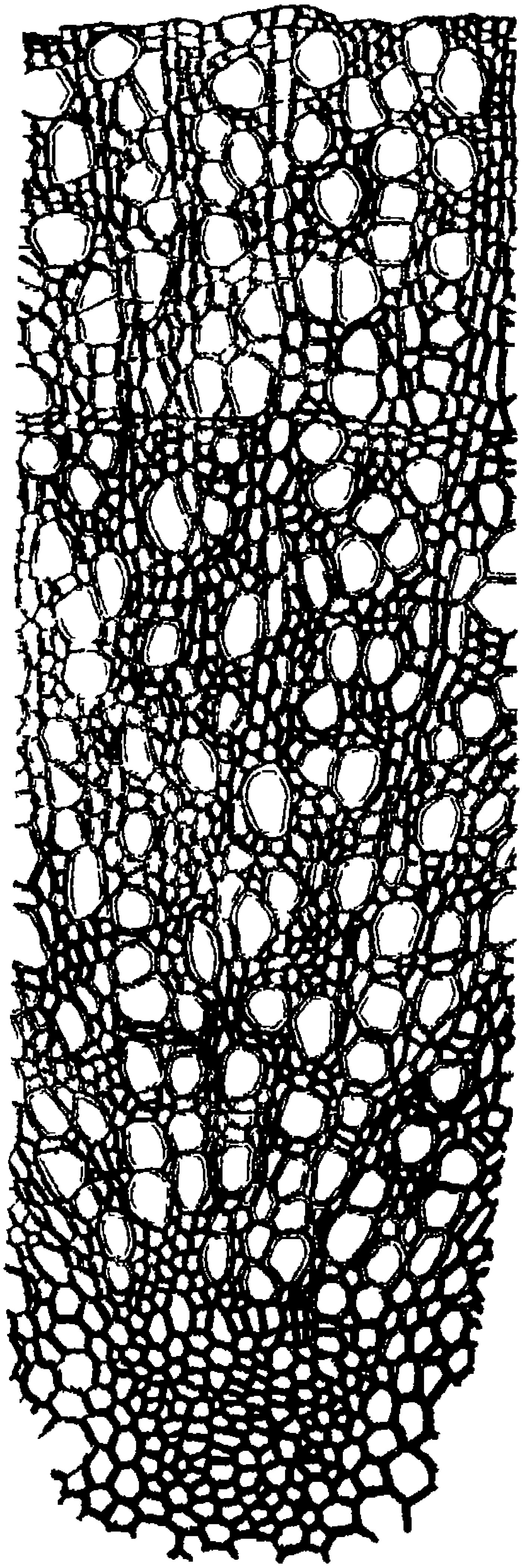

Fig 4 Transverse section of a two year old apple stem showing a large number of tracheae somewhat uniformly scattered throughout the xylem The vessels of one year are in close proximity to those of the next (x150)

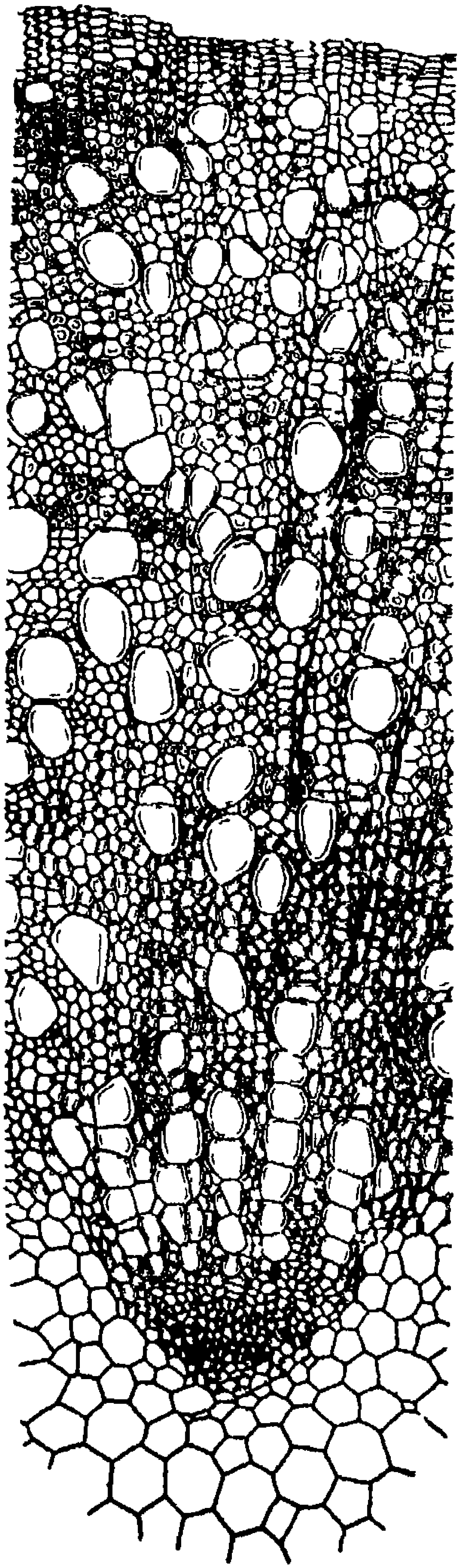

Fig 5 Transverse section of a one year old peach stem showing the tendency to ring porosity The tracheids are very thick walled and many of them separate one vessel from another and vessels of one season from those of another (x150)

TABLE 5

Data Gathered from Girdled and Ungirdled Canes of the Columbian Raspberry

		Green Weight	Dry Weight	Total Nitrogen	Total Nitrogen	Total Ash	Total Ash	Increase in Nitrogen	Increase in Ash
Sample Number		Grams	Grams	Per Cent Dry Matter	Grams	Per Cent Dry Matter	Grams		
Ungirdled cane	1	17 6	11 85	1 15	1363				
" "	2	16 0	8 26	98	0809	1 63	1346		
" "	3	16 6	10 92	87	0950				
" "	4	15 9	8 97	1 27	1139	2 87	2579		
" "	5	15 2	8 52	82	0698				
Average		16 3	9 70	1 02	0992	2 25	1962	1 00	1 00
Girdled cane	1	50 0	28 2	2 07	5937	4 08	1 050		
" "	2	83 5	23 5	1 43	5434				
" "	3	110 4	34 1	1 08	3682				
" "	4	116 0	44 1	1 00	4410	6 82	2 326		
" "	5	147 1	58 5	1 59	9301				
Average		101 4	37 7	1 43	5753	5 45	1 738	4 83	8 86

Thus, taking as unity the average nitrogen content of the dormant canes analyzed at the time of girdling, the girdled canes at the end of the season showed an average of 5 8 times more nitrogen The increase in ash content of the girdled over the ungirdled canes was 7 01 times

The Columbian raspberry showed similar results The girdled canes had an everage of 4 83 times more nitrogen and 8 86 times more ash than the dormant cane checks It is interesting to note that in the Cuthbert, as well as the Columbian canes, not only the absolute amounts of ash and nitrogen were higher in the girdled canes but the percentage composition was higher also This is, of course because the girdled canes possessed many leaves

The anatomical studies are in part reported in figs 2 5 The grape, (Fig 2), as well as the Cuthbert raspberry (Fig 3) stem sections, are shown with the bark intact, while the apple (Fig 4) and the peach stem (Fig 5) sections are shown as though they were girdled, that is, with the bark removed Thus these latter sections represent the complete xylem development and about one third of the pith

The grape seems to be very well suited to girdling experiments, (Fig 2) Its tracheae are very large and border the cambium region directly These vessels are so large that little difficulty is encountered in seeing them with the unaided eye The fact that they closely border the cambium is important when it is remembered that the next season's vessels will be laid down not more than one or two cells away from these vessels In the grape, the tracheids between the tracheae are rather thin-walled and therefore would be fairly permeable to water

The raspberry stem (Fig 3) likewise has fairly large and numerous tracheae These also are formed throughout the growing season, and thus are distributed throughout the wood A few of these vessels will be in rather close contact with the vessels of the succeeding season The walls of the tracheids are somewhat thicker than those of the grape and furnish more resistance to a stream of water passing through them These tracheids, as well as those of the grape, have relatively few pits

The apple stem (Fig 3), although woody, shows a very marked tendency to produce tracheae throughout the seasonal growth Especially significant is the fact that some tracheae are at the point of the cambium, so that if a girdle were made, the vessels would be exposed The vessels of the next season come in close contact with some of the preceding season Thus, one or at most, two tracheids separate the vessels of the successive rings of growth. These tracheids have fairly thick walls.

The peach (Fig. 5) is perhaps the least favorable subject for experimentation of this type. Its vessels are not numerous and are relatively small in diameter, especially those found in the late wood. There is a pronounced tendency for the peach to have its tracheae distributed through the early season wood rather than in the later season wood. The vessels do not border the cambium but are separated from it by at least six, or sometimes more than a dozen, very thick-walled tracheids. A casual glance at the cross section of the stems of the apple and peach will at once reveal the general openness of the apple wood as compared with that of the peach wood.

The plum and cherry show even more striking tendencies to produce ring porous wood, that is, to produce tracheae during the early season growth and *chiefly* tracheids during the later growth. Such a distribution of tracheae will make any lateral transfer of water very difficult as compared to the uniformly porous wood of the apple or grape.

DISCUSSION

The data certainly indicate that after the canes or twigs were girdled the portions above the girdles continued to obtain mineral materials and nitrates from below. Since a ring of phloem was removed, it is quite clear that the xylem served as a channel through which these materials moved. Why, then, are the conclusions of this paper so different from those obtained from data compiled by Curtis?

Perhaps the most obvious reason for this is the fact that the canes used as controls in the works of Curtis are not comparable with those reported in the present paper. In the experiments reported here, canes or twigs were selected in pairs, one cane or twig of each pair was girdled while the other was removed for analysis at *that time*. Curtis also selected his twigs in pairs, girdled one and allowed the paired twig to remain on the plant until the time the girdled twig was removed. Thus using the former system of controls, one can determine how much mineral material and nitrogen was in the portion of the cane above the girdle at the time the girdle was made. At the end of the experiment an analysis of the girdled shoot will determine the amount of these materials in the cane and the difference between the first and second analyses will show the amounts of materials which must have traveled through the xylem, since the continuity of the phloem tissues had been broken by the girdle.

Using Curtis controls, no data as to the beginning composition are obtained, and analysis at the termination will show, as Curtis concludes, that girdling the stem interferes with the upward movement of mineral and nitrate solutes It does not, however, indicate that these solutes move chiefly through the phloem, as Curtis states, since he makes little attempt to find what quantities of solutes move through the girdle In other words, his experiments do not support his ultimate conclusions

It may be well to consider therefore, why girdling interferes with the development of the parts above the girdle Such plants as the peach, cherry, plum, etc are not satisfactory plants for girdling experiments, while girdling such plants as the raspberry, grape, etc seems to have slight effect on further development The apple and pear seem to be somewhat intermediate in their response to girdling The reason for these individual differences, perhaps, must be looked for in the structure of the individual plants That such may be the case is suggested by Figs 2-5 The raspberry and grape, as noted above, have large tracheae, which are found directly bordering the cambium The subsequent development of xylem will bring more tracheae in close contact with the older vessels The peach, on the other hand, shows decided tendencies toward ring porosity, that is to say, the large vessels are formed early in the season and are followed by a considerable development of very thick tracheids which will separate the new vessels of the next season from those of the preceding season The apple is intermediate with respect to the grape and the peach The vessels of the apple are numerous and evenly distributed throughout the season's development, and thus the tracheae of one season will be separated from one another or those of the subsequent season's growth by one or two tracheids The distribution and structure seem, therefore, to be associated with the success enjoyed by these plants in girdling experiments

Some workers have thought that girdling tends to excite secretion by the living cells in the xylem and hence there is a tendency for the vessels to become plugged Curtis, however, shows this to be incorrect

It may be well to examine the effects which girdling has on the physiological process of the ascent of sap Ordinarily, the most recently formed vessels are the channels through which the chief movement of water takes place A reason for this may be inferred from the anatomy of the plant The leaf traces of one season are continuous with the cauline xylem of the same season On that account the leaves will draw their water from below through the paths of least resistance It would seem probable that these paths are in those vessels which are continuous with the leaf traces, and as noted above, these would be the ones more recently formed, or at least those of the present season That water movement takes place in part through some of the older wood is indisputable, but before the water moving through the older wood can reach a leaf, it must of necessity be transferred laterally to the xylem which is continuous with the leaf traces

If a strip of bark from around the stem is completely removed, the cambium is destroyed Of course this implies that at that point no new xylem can be formed However, the leaf traces forming in the portion above the girdle will again join the cauline xylem, but the xylem of the present season is not continuous with corresponding xylem below the girdle In fact, the activity of the cambium in the grape stem below the girdle is stopped Therefore, it is necessary for the entire movement of water to be drawn upward through the older vessels and be transferred laterally to the new xylem development above the girdle The upward movement of the water would encounter more resistance than it would were it moving through the new xylem from the roots to the leaves No matter how a plant is constructed a girdle hinders that upward movement of water and its solutes The relatively greater efficiency of some plants in girdling experiments as compared with others is perhaps due to the peculiar arrangement of the xylem vessels It follows then that lateral transfer from one year's xylem to the next will be easier in such stems as the grape and raspberry where the xylem vessels are large, numerous, and close together, than in such plants as the peach, where vessels are smaller, grouped in the early season woods, and where the vessels of consecutive years are separated by many (6-12) thick-walled tracheids In other words, the movement of water and its solutes will suffer much more resistance in going from one year's growth to the next in the peach than it will in the apple, and more in the apple than it will in the grape or the raspberry

It seems probable, therefore, that the soil solutes move upward in the plant in the water stream It is difficult to interpret the results of Auchter (1) and Bodenberg (2) regarding the lateral movement of mineral solutes Auchter used trees in his experiment and found that nitrogen added to one side of the tree was not transferred to the opposite side He also found that water could be transferred laterally about the stem It must be cautioned, however, that in trees, as Thomas (11) has observed, nitrates lose their identity as inorganic solutes in the small fibrous roots and can be found converted to organic forms When Auchter attempted to use ash analysis as the indicator of cross-transfer, he found it "unsatisfactory" Since the xylem water apparently carries the inorganic solutes, it remains an open question whether or not such solutes can be transferred laterally

SUMMARY

1 Chemical and anatomical studies are reported regarding the translocation activities of *Vitis vinifera, Rubus occidentalis, Rubus idaeus* var *strigosus* (Cuthbert), *Rubus neglectus*, (Columbian), *Pyrus Malus, Prunus americana,* and *Prunus Persica*

2 When the stems of the grape, raspberries and plum were girdled to the xylem, the upward movement of ash constituents and nitrates continued

3 The conclusions of Curtis are criticized as being in part unrelated to his data

4 An attempt is made to justify Curtis' conclusion that a girdle hinders the upward movement of soil solutes It seems that the distribution of tracheae in the seasonal development of xylem is to a large extent the factor which determines the ease with which plants can tolerate girdles

5 Since ash solutes are apparently carried by the xylem stream, it is difficult to understand the conclusion of Auchter, that although water can move laterally around the stem, solutes do not In view of the conclusion reached by Thomas, that nitrates are converted to organic nitrogen in the fibrous roots, it seems probable that Auchter's conclusions are valid only for organic materials which apparently move in the phloem tissues It is probable that they are non-valid for the mineral materials which he found unsatisfactory as criteria of lateral transfer of inorganic materials

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STUDIES IN LOCAL IMMUNITY[*]

L A Barnes[**]

The recent hypothesis of Besredka is of interest in connection with certain immunological problems According to his conceptions, there is a more or less specific affinity between each pathogenic microorganism and certain "receptive cells" in the body For example, certain cells in the walls of the intestinal tract have a special attraction for organisms causing enteric diseases Susceptibility and immunity to anthrax in guinea pigs are likewise considered to be limited largely to the cutaneous system The method of immunization recommended, therefore, requires the application of the immunizing agent to the tissues at the local portals of entry Complete protection is effected when the affinity of the receptive cells has been entirely satisfied The part played by the known antibodies consequently becomes of little or no significance Immunity is, therefore, entirely a local phenomenon It is claimed that the affinity of the receptive cells may be satisfied by the application of filtrates of old broth cultures of homologous organisms to those tissues directly concerned As a result of these ideas, the value of so-called "antivirus" has been emphasized in producing immunity against various diseases

A review of the literature dealing with local immunity reveals conflicting evidence regarding Besredka's hypothesis It was deemed advisable, therefore, to obtain further experimental information concerning certain claims made by this author

In a general way, the material presented may be divided into five sections (1) comparisons of the effectiveness of various methods of administering bacterial vaccines, (2) test of Besredka's thesis that oral vaccination results in a specific impermeability of the intestinal mucosa, (3) the antigenic and protective action of bacterial vaccines and of Besredka's filtrates applied to the skin in the form of wet dressings, (4) the nature of Besredka's "antivirus", and (5) test of Besredka's proposition that "the susceptibility of the guinea pig to anthrax is limited principally, if not exclusively, to the cells of the skin"

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[*] This is an abstract of a dissertation submitted to the Faculty of the Graduate School of the State College of Washington in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Bacteriology June 1929

[**] Now located in the Dept of Hygiene and Bacteriology in the School of Medicine of Western Reserve University Cleveland, Ohio

As a result of a series of experiments dealing with the effectiveness of various methods of administering bacterial vaccines, some evidence was obtained that the intestinal wall may in some cases become impermeable to the organisms in the fecal contents This is not true in all cases, however The demonstration of agglutinins in the intestinal wall and feces of orally immunized animals for colon bacilli suggests a partial explanation for the impermeability of the mucosa for these organisms Results were inconclusive in an attempt to demonstrate a superiority of the subcutaneous method over the oral method in stimulating the production of agglutinins The intravenous route was superior to the other methods in this respect No superiority in agglutinin production was noted in animals treated with bile before per os vaccination as compared with those not receiving bile

Intravenous vaccination of rabbits with native fecal bacteria resulted in some cases in the apparent disappearance of homologous organisms from the intestinal tract Oral administration of vaccine to another series of rabbits failed to accomplish these results These observations support the view that oral vaccination is less effective than parenteral vaccination and furnishes evidence against the efficiency of local intestinal immunity Further work is necessary, however before definite conclusions can be drawn

Experiments on a series of rabbits in which the animals were orally vaccinated with avicida vaccine and later with paratyphoid vaccine failed to produce evidence against the supposition that per os administration of vaccine results in a specific impermeability of the intestinal mucosa It was found that oral administration of paratyphoid vaccine resulted in the appearance of both homologous and heterologous agglutinins

Cutaneous applications of dressings moistened with vaccines of typhosus or coli failed to bring about the appearance of agglutinins in the blood of a human volunteer

The intravenous injection of coli antivirus filtrates into rabbits resulted in the appearance of homologous agglutinins in the blood Intracutaneous injections and cutaneous wet dressings of the same filtrate failed to produce an increase in agglutinins in the skin of rabbits, although a certain degree of absorption apparently occurred as evidenced by rises in the agglutinin titer of the blood serum

In two human cases, treated for boils on the face by the use of autogenous antivirus filtrates, the application of wet dressings failed to produce local immunity within twenty-four hours, as has been claimed by others

Immunological tests on a small number of rabbits failed to support the contention that antivirus is specific, providing the assumption that biologic specificity is inherent only in protein substances is accepted

Further tests on the nature of antivirus indicated that the inhibitory action of filtrates is not specific The artificial digestion of broth by enzyme action produced evidence that the inhibitory factor results from decomposition of protein in the medium rather than from disintegration of bacterial cells The failure to obtain antivirus in synthetic medium cultures containing no protein further supported this view When peptone was added to the synthetic medium, however, the inhibitory factor was obtained following the growth of the same organisms

Besredka believes that the susceptibility of guinea pigs to anthrax is limited largely, if not entirely, to the cells of the skin If this is true, the protection of the skin at the site of subcutaneous injection of the organisms should prevent infection in such animals

Consequently, a series of guinea pigs was injected subcutantously with a broth culture of *B anthracis*, both before and after injections of gentian violet solution into the tissues at the site of the needle puncture through the skin Controls were injected with culture alone and others with dye alone The results produced satisfactory evidence that the susceptibility of guinea pigs to anthrax is not limited to the skin Animals in which the skin injury is protected from infection will succumb to typical anthrax Cultures from the dye stained areas failed to show krowth while those from the edematous tissue at the point of localization resulted in pure cultures of *B anthracis*

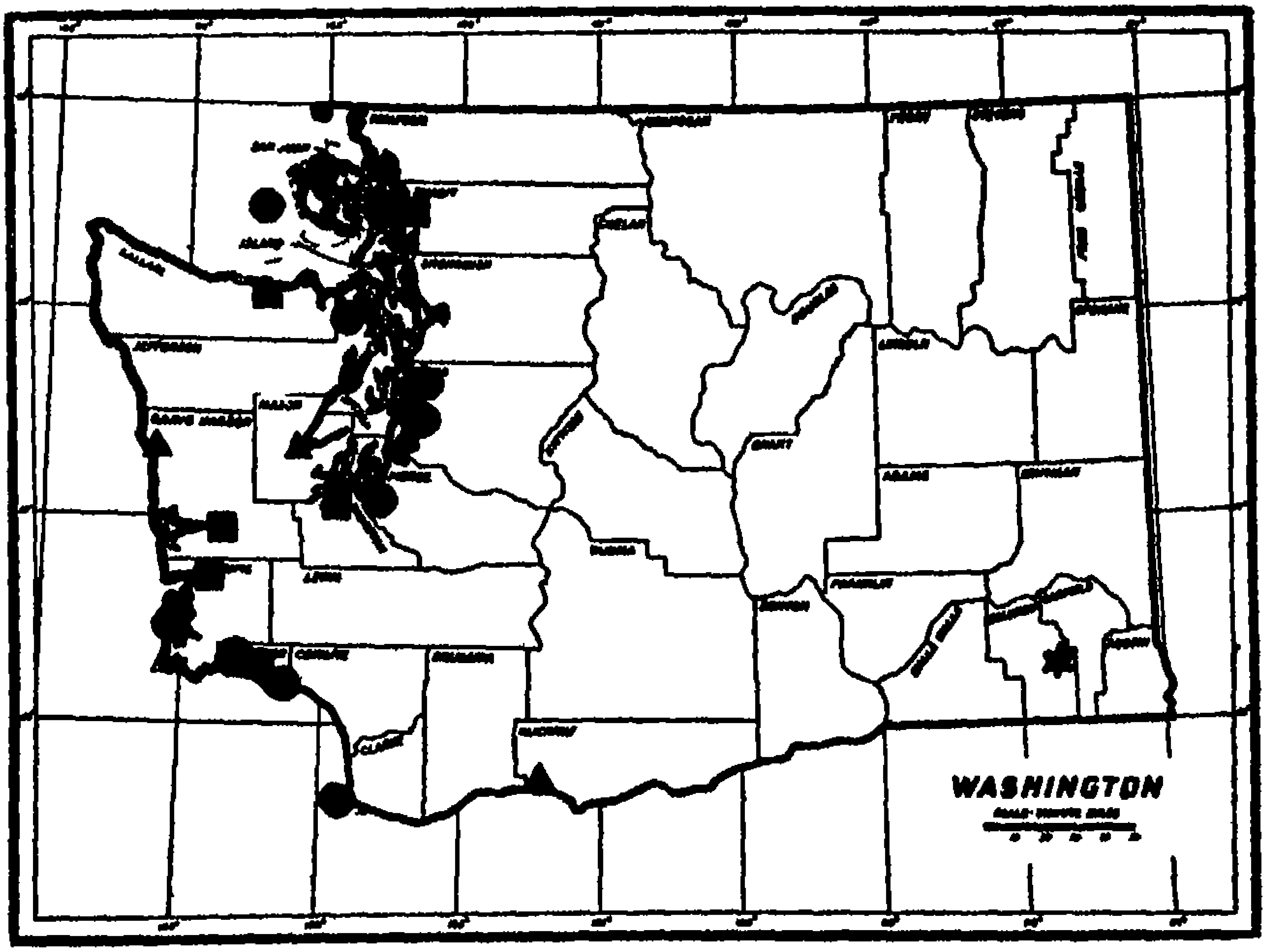
In conclusion, it may be stated that while intravenous vaccination is apparently more effective in stimulating agglutinin production and immunity, the comparative value of oral and subcutaneous methods remains to be determined The factor in broth culture filtrates which inhibits bacterial growth is apparently non-specific It does not appear to be liberated from the bacterial cells but seems to be due rather to the decomposition of proteins in the medium Anthrax infection in guinea pigs is not entirely dependent upon the susceptibility of the skin to the organisms

NEW AND NOTEWORTHY NORTHWESTERN PLANTS*

PART 5

HAROLD ST JOHN

(Received for publication August 14 1930)



Map showing area surveyed

JUNCUS EFFUSUS L., var **caeruleomontanus** n var Plants densly tufted, rather slender, 6-7.5 dm tall, culms rigid, finely many sulcate throughout, 1.3-2.2 mm in diameter at the top of the sheaths, sheaths close, firm, scaberulous, striate to the tip, castaneous throughout or sometimes paler laterally just below the tip, the uppermost 45-75 mm long, dull instead of lustrous, involucral leaf 7-16 cm long, inflorescence small loose elongate, 2-5 cm long, 9-30 mm wide, perianth segments ascending linear-lanceolate, subulate-tipped, the median third rigid, pale green, 3-ribbed, the marginal thirds plane, scarious, brown, sepals slenderly acuminate, 2-2 8 mm long, petals equal and similar, but at tip oblong-lanceolate, apiculate, capsule greenish-brown, trigonous obovoid, short apiculate, equaling the perianth or nearly so

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* Contribution No 29 from the Botany Department of the State College of Washington

Caulibus tenuibus 6-7 5 dm altis 1 3-2 2 mm diametro, cataphyllis castaneis opacis 45-75 mm longis, sepalis rigidis viridibus trinervosis, marginibus brunneis scariosis, capsulis perianthium aequantibus apiculatis

WASHINGTON swampy ground Tucannon River Valley Columbia Co Wenaha [now the Umatilla] Forest Reserve, Blue Mountains, July 26, 1913, *H T Darlington* 336 (type in Herbarium State College of Washington)

This new variety comes closest to var *gracilis* Hook of those as yet described The following contrasting characters will serve to differentiate the two Var *caeruleomontanus* has the sheaths dull, the upper ones 45-75 mm long, the culm 1 3-2 2 mm thick at base, and the perianth rigid, with the broad margins brown, scarious, and not wrinkled On the other hand, var *gracilis* has the sheaths lustrous, the upper ones 7-11 cm long, the culm 1-1 5 mm thick at base, and the perianth soft, when dry more or less wrinkled and curved, with the margins almost scarious

Juncus effusus and its varieties are widely distributed and locally abundant over many parts of the northern hemisphere It received monographic treatment[1] by Fr Buchenau in 1906 Later came an excellent critical revision[2] by Profs M L Fernald and K M Wiegand, which clarified the taxonomic position of the North American variations, and called attention to their clearly delimited geographic ranges They excluded true *J effusus* from North America, but admitted nine varieties More recently Drs L R Abrams and F V Coville have covered this species in the far west[3] They admit var *brunneus* as common along the coast The three other west coast varieties, they neither admit nor place in synonomy True *J effusus* they include from "swamps and moist places, Canadian to Upper Sonoran Zones, Common throughout the Pacific States except the desert areas" Ranges as stated in the Illustrated Flora of the Pacific States often have a strong Californian emphasis, in that the detailed limits are given for that state, while for Oregon and Washington, they are omitted or very briefly stated The writer has seen no true *J effusus* from British Columbia, Washington, or Oregon, but, on the contrary, has seen good material of var

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[1] Engler, A Pflanzenreich IV, fam 36 135 137 1906

[2] Rhodora 12 81 93 1910

[3] Abrams, L R, Ill Fl Pacific States 1 358 1923

gracilis, of var *pacificus*, and of var *brunneus* They seem clear, well delimited varieties Dr W L Jepson recognizes several of the varieties as occurring in California,[4] but also admits the species *J effusus* It will be recalled that Fernald and Wiegand excluded the species proper from North America Not enough Californian material has been studied by the writer to enable him to express an opinion whether or not the true *J effusus* occurs in that state However, it does not seem to occur in Washington or Oregon Nor is the species or any of its varieties "common throughout" these two states Certain varieties are common along the sea coast and on the low swampy lands of the Puget Sound trench, and the lower Columbia River Until this present writing, there has been little evidence of any stations in the larger part of Washington which lies east of the Cascade Mountains The only record is for var *pacificus*, which Fernald and Wiegand cite from Waitsburg, July 31, 1897, *R M Horner* Dr B L Robinson of the Gray Herbarium has kindly loaned this specimen for rechecking After careful comparison and determination the writer is forced to admit that it is correctly named var *pacificus* It has an original Horner label which besides the quoted data, bears the habitat, "In water," and the number R474B502 Set 1 of the Horner collection which is in the Herbarium of the State College of Washington, does not include this number or species It was not cited by Prof C V Piper in his "Flora of the State of Washington" or by Piper & Beattie in their "Flora of Southeastern Washington and Adjacent Idaho" No subsequent collection has shown var *pacificus* as a native of the great interior part of Washington east of the Cascade Mountains The writer has verified the identity of the specimen and found its determination to be correct beyond question, but he has reasonable doubt as to its locality The banks of the Touchet River near Waitsburg should be carefully searched for this plant Unless this locality can be confirmed, it should be rejected as dubious, since all other records are from the low shores of the Pacific

Southeastern Washington has been intensively explored during recent years, but only one collector has gathered any *Juncus effusus* The collection here described as a new variety came from within forty miles of Waitsburg, but on the Tucannon River, an independent tributary of the Snake, not connected with the Touchet

Except for these two localities on the north slope of the Blue Mountains, *J effusus* and its varieties seem absent from eastern Washington and apparently so from eastern Oregon Waitsburg is at an elevation of 1,272 feet, and the Tucannon locality at about 2,000 feet The former is in an air line 170 miles and the latter 200 miles from the nearest west side station for the plant The intervening country is largely of the arid Upper Sonoran type

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[4] Man Fl Pl Calif 199 1925

Botanists familiar with the regions east of the Cascades will stoutly deny that they are all deserts The sizeable desert areas existing there are all of the Upper Sonoran They, together with the very extensive Arid Transition and the Canadian areas, make up most of the eastern portions of these states Hence, even with the qualification "except the desert areas," the statement by Abrams and Coville of the range of *J effusus*, as "Common throughout the Pacific States," is far from accurate for Oregon or Washington

The name for the new variety has been coined in allusion to its geographic location, the Blue Mountains, from the Latin *caeruleus*, blue, and *mons*, mountain

ERYTHRONIUM GRANDIFLORUM Pursh, var **pallidum** new name

This plant is abundant and well known in the region from the Rocky Mountains to the Pacific In recent years it has been called *E grandiflorum* Pursh, var *parviflorum* Wats, or *E parviflorum* (Wats) Goodding The specific name given by Prof Goodding is based entirely upon the varietal name of Dr Watson's He, in turn, based his variety *parviflorum* upon E *Nuttallianum* Regel, (not R & S, which equals *E americanum*), Gartenfl 20 227, t 695, figs 1, 2, 1871 This is a good colored plate showing a 1-flowered plant with unmottled green leaves, yellow perianth parts and purple stamens It is clearly identical with the earlier *E grandiflorum* Pursh, and hence different from the white-anthered plant so long called var *parviflorum* Watson also cites *E grandiflorum* Murray, Gard Chron n s 1 fig 173, 1874 This plate is not colored, and the accompanying discussion makes no mention of the color of the anthers, but, in absence of proof, there is no reason to assume that it is different from *E Nuttallianum* Regel or *E grandiflorum* Pursh The plant came from near Salt Lake, Utah *E grandiflorum* Pursh, var *parviflorum* Wats rests upon these two citations One is certainly *E grandiflorum* Pursh, and the other presumably so At the Gray Herbarium where Dr Watson worked, there are no specimens labeled var *parviflorum* in his handwriting He mentioned no type, so there seems no way to save his varietal name from rejection

These facts make it clear that var *parviflorum* Wats is a synonym of *E grandiflorum* Pursh There seem to be no available synonyms for the white-anthered plant

The writer is very familiar with both plants in the field *E grandiflorum* is very abundant on the grassy plains of eastern Washington and in the low mountain region of northern Idaho Each spring he has examined hundreds of living specimens of this lovely flower The white anthered one grows on the middle and upper slopes of the mountains and, soon after the snow melts, dominates great areas of the meadows This, too, has been given extensive field study From the published descriptions in the standard floras and monographs, a considerable list of the differences used to separate the two plants has been compiled Field and herbarium study have caused the rejection of most of these as not in reality contrasting or distinctive The following points do stand examination *E grandiflorum* has the anthers reddish-purple, turning brownish on dehiscence, the perianth averaging a little over 3 cm in length, stems commonly 1-2-flowered, but on old, undisturbed plants, 3-10-flowered, abundant in, and characteristic of, the Arid Transition, but occasional in the Upper Sonoran and up to the Hudsonian, and it occurs east of the Cascade Mountains in eastern British Columbia, Washington, and Oregon, and inland to Montana, Wyoming and Utah The other plant has the anthers white, turning yellowish on dehiscence, the perianth averaging about 3 cm in length, the stems 1-2-flowered, and it occurs abundantly and characteristically in the Canadian and Hudsonian, but appears also in the Arid Transition, and occurs from the Coast Range Mountains of Vancouver Island, British Columbia, the Olympic Mountains, Washington, south to Humboldt County, California and inland to Montana, Wyoming, Colorado and Utah Upon analysis the distinctions are not very strong The presence of a purple pigment in the anthers and pollen grains of one plant is the only really tangible character The occasional production of numerous flowers by old vigorous plants of *E grandiflorum* is suggestive, but not useable as a constant character The size of the perianth has been much emphasized by other writers However, in *E grandiflorum*, the extremes are from 2-5 cm while in the other plant, from 2-4 5 cm This does not provide a character that will serve. The zonal distribution has been considered important *E grandiflorum* is abundant on the grassy plains of the Arid Transition, up into the timbered portion, and not uncommonly up into the Canadian For one thousand feet or so it may overlap the white-anthered plant, which continues on from there to snow line in the Hudsonian There are still more puzzling occurrences *E grandiflorum* is the only one recognized near Pullman, Washington It is so abundant in the spring that school children bring in huge bouquets of it every year The writer often sent a group of his students to study the dimorphism of the anthers of this species Just as in most species in the genus, there are many plants in the same colony with 6 long stamens, many with 6 short stamens, and others with 3 long and 3 short ones The "Timber Culture" three miles northeast of Pullman has been spared from plowing, so *Erythronium* abounds On April 9, 1927, Miss Rocelia Palmer, while observing hundreds of the plants, found one with white anthers, not otherwise different from its fellows Close observations by many students in this small spot had not, during many years, revealed any others If this white-anthered plant is to be considered a species, why should it appear in this colony in the bunch grass prairies of the Palouse Country?

Similarly, when collecting on the highest ridges of the Blue Mountains in southeastern Washington at 5500 feet elevation, the writer found the plants on a gravel slope near a retreating snow bank Both types were found growing there side by side, though the area is in the Hudsonian Zone, at the upper altitudinal limit of the montane plant The purple-anthered *E grandiflorum* from there is *St John* & *Smith* 8344, and the white-anthered one is *St John* & *Smith* 8343

These sporadic occurrences both at the lower and upper altitudinal limits inhibit the supposition that one of the two is an ecological response to climatic or edaphic conditions of mountain or lowland

The geographic range of the two plants comes very near to coinciding, though one does fail to cross the Cascade-Sierra range, while the other goes the one hundred miles or so to the Pacific

The occurrence and distinguishing characters of the two plants have been discussed in considerable detail since it seems necessary to evaluate them anew The morphological differences are slight The zonal distributions partly overlap, and each plant may appear sporadically at the farthest outpost of the other The total geographic ranges differ but little, and come very near to coinciding The writer is forced to the conclusion that one should be allocated as a variety of the other

The new name, var *pallidum*, is from the Latin meaning pale in color and is given in allusion to the pale anthers

Sufficient descriptive material for the newly named variety is included in the previous paragraphs Since the plant is redefined, it is desirable to name a type specimen and to cite the typical specimens examined

British Columbia Chase April 28, 1919 Aug 18, 1919, *J R Anderson*, open [places] Creston, May 2, 1908 *J R Anderson*, open places on mountain side, Crawford Bay, *L C Harrison*, Enderby, June 28, 1907, *J R Anderson*

Washington rock slide near snow-bank Horseshoe Basin, Chelan Co July 13 1923 *H St John* & *L Ridout* 3670 (type in Herb State College of Washington) Olympic Mts Clallam Co June 1900 *A D E Elmer*, Silverton, *L A Bouck* 189 6000 ft Goat Mts Mt Rainier July 23 1894 *O D Allen* 82, wet meadows 6500 ft alt Mt Rainier, Aug 1895 *C V Piper* 2100 in part, Wenatchee, April 30, 1899, *K Whited* 1053 shady places, alt 5300 ft, Wenatchee Mts June 20 1903 *J S Cotton* vbjf, Ellensburg April 24 1897, K Whited, meadows Chinook Pass June 23 1926 *F L Pickett* 1361 Appleton, May 5 1911 *R K Beattie* 3883, open woods, clay Dalkena May 11 1923, *C H Spiegelberg* 83, open woods, Newport May 5, 1923 *C H Spiegleberg* 85, Pullman April 9 1927, *R Palmer*, edge of woods, 4000 ft, Anatone, May 30, 1928 *H St John* & *R Palmer* 9593, Blue Mts, Walla Walla Co, July 1896, *C V Piper* gravel slope near snow 5500 ft, Stayawhile Spring, Columbia Co, *H St John* & *C P Smith* 8343 open pine woods Pomeroy May 2 1921 *W D Courtney*, near snow bank Squaw Spring Trail, Garfield Co July 24 1913 *H T Darlington* 159 open fields Anatone May 19, 21 1922 *H St John* & *Rex H Brown* 4213, and 4856

Idaho 5600 ft Experiment Station Lookout Priest River, June 4, 1925, *J C Witham* 45, rocky hillside Albany Falls May 13 1923 *C H Spiegelberg* 84, Soldier's Camp, Lolo Trail, July 17, 1902, *C V Piper* 4085

Oregon near snow 5500 ft, Mt Hood, Aug 7 1927, *C English Jr* 858

Colorado above timber line at Cameron Pass Aug 1, 1899, Herb State Agric College, Col 2461

University of Hawaii,
Honolulu, Hawaiian Islands

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RESEARCH STUDIES of the STATE COLLEGE OF WASHINGTON

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DRYDEN'S INFLUENCE ON THE VERSIFICATION OF *LAMIA*

C A LANGWORTHY

In his introduction to his edition of *The Poems of John Keats,* E de Selincourt makes the following statement

> For his model in *Lamia* he [Keats] turned to the Fables of Dryden, the best modern example of the use of the heroic couplet in narrative verse The versification and style of *Lamia* give clear evidence that he had made a careful study of Dryden In contrast with the earlier couplets of the 1817 volume and of *Endymion* his employment of the run on line and the feminine and weak endings is now carefully controlled, and he trusts to a careful use of the triplet and Alexandrine to give his verse the necessary variety[1]

Again in his notes on *Lamia* Mr Selincourt writes

> The versification is closely modeled upon the Fables of Dryden, from which Keats learned how to relate his metre with his sentence structure and to use both the triplet and the Alexandrine with striking success[2]

That Keats actually did make a study of Dryden's Fables and that *Lamia* affords evidence of such a study it is not the purpose of this article to deny What I wish to do is to determine by certain objective tests[3] to what extent the handling of the couplet in *Lamia* differs from that in *Endymion* and how closely, in that difference, Keats was approximating the particular style of Dryden's Fables as distinguished from Dryden's general handling of the couplet

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[1] London, Methuen and Co 1926 p lii

[2] Ibid., p 458

[3] The main tests employed in this article are a minor modification of my system of verse-sentence analysis, designed to apply to the heroic couplet For an explanation of the complete system see my Verse Sentence Patterns in English Poetry " Philological Quarterly, VII 283 and my forthcoming article "A Verse-Sentence Analysis of Shakespeare's Plays " in PMLA. In the latter article I make an extended criticism of such tests as those of the run-on line light and-weak endings, etc The main defect of all these tests is their almost exclusive concern with line-endings and their disregard of the relation of grammatical structure to the line as a whole

I am applying my tests to 500-line passages chosen respectively from two poems of Dryden and two of Keats From Dryden I choose *Absalom and Achitophel,* as an illustration of one of the most famous of his handlings of the heroic couplet outside the Fables, and *Palamon and Arcite* because, in paraphrasing Chaucer's poem, Dryden was exposed to the example of a looser handling of the couplet than that to which he was accustomed Here, if anywhere in the Fables, we might expect the maximum difference from the style of *Absalom and Achitophel* From Keats, in addition to *Lamia,* I am choosing two selections from *Endymion,* the poem which Selincourt cites as the main example of Keat's earlier handling of the rhymed couplet That these 500-line passages are long enough to be typical of the stylistic practices in the complete poems from which they are taken should be convincingly illustrated by the statistical similarities between the two *Endymion* samples

First, then, let us note the evidence in *Lamia* of Keat's indebtedness to Dryden's Fables in the handling of feminine rhymes, triplets, and Alexandrines

In the first 500 lines of the first book of *Endymion,*[4] I find 11 feminine rhymes, in the first 500 lines of Book III, I find 7 Since there are no feminine rhymes in *Lamia* and none in the samples from either of Dryden's poems, it wil be seen that Keats's handling of rhyme in *Lamia* is somewhat different from that in *Endymion* and that the difference is in accord with Dryden's handling of rhyme The absence of feminine rhymes in *Lamia* shows, however, no special influence of Dryden's Fables since such rhymes are entirely absent in the passage from *Absalom and Achitophel* as well as in the passage selected from the Fables

But in the use of Alexandrines and triplet rhymes the special influence of the Fables upon *Lamia* is clearly apparent The *Absalom and Achitophel* selection has no Alexandrines, the *Palamon and Arcite* selection has 17 The *Endymion* selections have no Alexandrines, the *Lamia* selection[5] has 26 Of triplet rhymes there are in the *Absalom*

---

[4] In counting the first 500 lines of Book I I omit the hymn to Pan ll 232 306 because it is not written entirely in the rhymed couplet

[5] Lamia is a poem of 708 lines For the convenience of dealing with comparable units I am applying my tests to the first 500 lines of this poem I have made a separate count for the last 208 lines but the differences are not such as to require separate notation

and Achitophel selection only 4, in the *Palamon and Arcite* selection there are 13 There are none in either of the *Endymion* selections, in the *Lamia* selection, however, there are 9 triplet rhymes and 1 quartet

In both Dryden and Keats the use of the Alexandrine is confined to the last line of a rhyming group The tendency of the Alexandrine to occur in triplet rhymes is much more pronounced in Keats than in Dryden In the *Palamon and Arcite* selection only 4 of the 13 triplets have Alexandrine lines, in the *Lamia* selection the 1 quartet and 8 of the 9 triplets have Alexandrines as their last line

Since the influence of Dryden's Fables upon Keats's *Lamia* is quite evident in the use of triplet rhymes and Alexandrines, one is naturally disposed to accept Selincourt's statement that, in writing *Lamia,* Keats learned from the Fables "how to relate his metre with his sentence structure" Let us see to what extent this statement is confirmed by objective tests

In the several tests which follow, the unit of grammatical structure employed is what I call the clause-group the independent clause with whatever dependent clauses may be attached to it In dealing with the relationship of line and syntax, I find such a unit more valid than the sentence itself because the number of independent assertions which an author includes in his sentence is largely the result of arbitrary choice

In my first test I record the number of such clause-groups in each selection and the relative number of clause-groups ending at different points within and at the end of the line For convenience I select the perfectly regular iambic-pentameter line as a scale Such a line, of course, has ten syllables Of these the syllables with odd numbers are the unaccented, those with even numbers the accented Because I am concerned with the relative positions in the line where clause-groups end, I ignore reversals of accent and scan trochees as iambs Spondees and pyrrhics are similarly dealt with Where substitutions of anapests for iambs occur, I record clause-group endings falling upon either of the unaccented syllables of a foot as occurring upon the odd syllable of that foot Thus, clause-groups ending upon the first or second light syllables of the third foot are both counted as ending upon syllable 5 Similarly, since I have made a separate count of feminine endings, all clause-groups terminating with the line are recorded as ending upon syllable 10 The results are revealed by the following table

Number and Position of Clause-Group Endings

	Absalom and Achitophel	*Palamon and Arcite*	*Endymion Book I*	*Endymion Book III*	*Lamia*
Syllable 1	0	0	0	0	0
Syllable 2	1	1	1	2	9
Syllable 3	0	2	3	4	8
Syllable 4	6	15	17	16	19
Syllable 5	1	3	21	23	15
Syllable 6	4	14	20	42	14
Syllable 7	1	0	15	25	12
Syllable 8	1	0	0	4	0
Syllable 9	0	0	1	2	0
Syllable 10	196	211	91	137	136
Totals	210	246	169	255	213

The table reveals that clause-group endings falling upon syllables 1, 2, 3, 8, and 9 are rare in all the selections In the *comparative* frequency of clause-group endings upon syllables 2 and 3 *Lamia* differs from all the other selections, so that no light is thrown upon the problem of Dryden's influence by this difference For syllable 6 *Palamon and Arcite* shows a marked difference from *Absalom and Achitophel*, but the figures for the same syllable in *Lamia* and in the two *Endymion* selections show no special influence of the Fables upon *Lamia* For syllable 7 all the Keats selections agree in their sharp difference from the Dryden selections

The most significant differences, however, are revealed at syllable 10, the end of the line Here it is well to resort to percentages Of the total number of clause-groups in each selection, my figures indicate what percentage end at the last syllable of the line It is interesting to note that, in spite of the large difference between the two *Endymion* selections in the total number of clause-groups, and in spite of a considerable difference in the distribution of clause-group endings within the line, they show the same percentage of clause-group endings at the last syllable of the line, namely, 54- The *exact* agreement, of course, is a coincidence For all five selections the percentage of clause-group endings at the last syllable of the line is as follows

Absalom and Achitophel	*Palamon and Arcite*	*Endymion Book I*	*Endymion Book III*	*Lamia*
93+	86—	54—	54—	64—

From these figures it will be seen that the special influence of the Fables upon *Lamia* is measurably apparent, but that, in the percentage of clause-group endings at the end of the line, *Lamia is* considerably nearer to *Endymion* than to either *Absalom and Achitophel* or *Palamon and Arcite*

Since, however, it is not only the relation of line and sentence but also that of couplet and sentence which is involved in the problem of Dryden's influence upon *Lamia,* two further tests may profitably be applied In the combined movement of line and sentence, it must be evident that clause-group endings at the end of the first line of the couplet tend to break up the couplet unity even though the couplet may be closed at the end Accordingly, of clause-groups ending at the end of the line, I now record the percentage of those which end upon the *first* line of the couplet [*]

Absalom and Achitophel	*Palamon and Arcite*	*Fndymion Book I*	*Endymion Book III*	*Lamia*
16—	16+	55—	48+	21

By this test *Lamia* appears to be further from *Endymion* and closer to the Fables than by any test I have thus far applied It is not measurably closer to *Palamon and Arcite,* however, than to *Absalom and Achitophel*

But these statistics for clause-group endings at the end of the first line of the couplet afford exaggerated evidence of the resemblance between the versification of *Lamia* and that of the Dryden selections For in Dryden most of this species of clause-groups begin with the line as well as end with it, and are usually balanced by another clause-group which begins and ends with the second line of the couplet In *Lamia,* on the other hand, many of these clause-groups, as in *Endymion,* extend into this first line from a previous couplet

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[*] There are no instances in the selections of a clause group ending at the end of the first or second line of a triplet

To correct the implications of this test and to show that the difference in versification between Dryden and Keats is greater than that revealed by any of the tests so far employed, I shall now record the relative frequency of occurrence, in the five selections, of three types of the heroic couplet For convenience of tabulation, I label these types A, B, and C, respectively In type A a clause-group extends into the couplet from the preceding couplet and ends at some point within the first line of the couplet At this point another clause-group begins which ends at the end of the couplet

> estrange their altered hearts
> From David's rule and 'tis the general cry,
> "Religion, commonwealth and liberty"[7]

Such a couplet is open only at the beginning Type B is similar to type A except that the last clause-group is not complete at the end of the second line of the couplet but extends into the succeeding couplet

> and the dairy pails
> Bring home increase of milk And as the year
> Grows green in juicy stalks, I'll smoothly steer[8]

In type C[9] a clause-group comes to an end at some point within the last line of the couplet At this point another clause-group begins and extends into the following couplet

> and there had led
> Days happy as the gold coin could invent
> Without the aid of love, yet in content[10]

The following table reveals the number of each of these types of couplet in the five selections

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[7] Absalom and Achitophel, ll 197 198

[8] Endymion, I ll 46 47

[9] In all these types one or more clause-groups may occasionally intervene between the first and last clause-groups of the couplet

[10] Lamia, I. ll. 305 306

	Absalom and Achitophel	*Palamon and Arcite*	*Endymion Book I*	*Endymion Book III*	*Lamia*
Type A	3	3	7	17	11
Type B	0	1	27	20	12
Type C	0	0	30	31	17
Totals	3	4	64	68	40

It is this last table which, it seems to me, represents most clearly to what extent Keats learned from the Fables of Dryden "how to relate his meter with his sentence structure" The test is equally applicable to the relation between line and sentence and to the relation between couplet and sentence for it involves a classification of couplets on the basis of a measurable divergence between metrical and grammatical elements In each type the syntax diverges from both the line-unity and the couplet-unity Since all three of the types are varieties of the open couplet—an open couplet with a measurable meaning—I may now make the following numerical statement of the extent to which Keats learned from Dryden's Fables to relate his meter and sentence structure I may say that Keat's couplet in *Lamia* is only ten times more open than Dryden's couplet in *Palamon and Arcite,* whereas his couplet in *Endymion* is from sixteen to seventeen times more open In the relation of meter and sentence structure, *Lamia* is thus seen to be a *little* nearer to *Palamon and Arcite* than is *Endymion*, but obviously the versification of *Lamia* is still incomparably closer to that of *Endymion* than to the versification of *Palamon and Arcite*

It may, of course, be objected that so great a difference between the versification of *Lamia* and *Palamon and Arcite* should not be asserted on the basis of a test which does not involve all the lines in the selections[11] To deal with all the lines would involve far more details of my system of verse-sentence analysis than could be presented within the limited scope of this article But in any case it should be recalled that the figures in my last table represent couplets, so that the figures must be doubled to indicate the number of lines involved

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[11] A further objection might be that the handling of the couplet in Palamon and Arcite may not be typical of the Fables To meet this objection I have examined five-hundred line selections from Sigismonda and Guiscardo and The First Book of Homer's Ilias. In the former I find seven of type A and none of the other couplet types In the latter I find five of type A and one of type B

Furthermore, the difference between the couplets measured by this test in *Lamia* and those of its alleged model, the Fables, is even greater than my numerical statement indicates For it should be noted that three of the four open couplets recorded for the *Palamon and Arcite* selection belong to type A Now type A indicates a much less open couplet than either B or C Just as in the Italian sonnet the sestet is still felt to be a unit when, as often happens, it does not begin with the opening of the ninth line, so also a couplet is felt as at least a partial unit if its main clause-group begins before the first rhyme and ends at the second rhyme, even though this clause group does not begin at the first syllable of the line

The investigations embodied in this article confirm Selincourt's conclusion that, in writing *Lamia,* Keats was influenced by the example of Dryden's Fables in the avoidance of feminine rhymes, which were fairly frequent in *Endymion,* and in his use of the Alexandrine and of the triplet, neither of which is to be found in the representative selections from *Endymion* which I examined On the other hand, in the much more important matter of the relation of meter and sentence structure, I have shown that Keats learned from Dryden's Fables very little indeed, since *Lamia,* in this respect, is incomparably closer to *Endymion* than to *Palamon and Arcite* Accordingly, Selincourt's statement that in *Lamia* "The versification is closely modeled upon the Fables of Dryden" should be emended to read The versification is *slightly* modeled upon the Fables of Dryden

NEW AND NOTEWORTHY PLANTS OF THE PACIFIC NORTHWEST*

PART 1

George Neville Jones

(Received for publication December, 1930)

Sedum rupicolum n sp Perennial, stems erect, simple, smooth, 10-20 cm high, leafy near the base, leafless or nearly so above, leaves numerous, ellipsoid, or the young ones ovoid, the older ones curved upward, thick, glaucous, minutely papillose and pitted, obtusely pointed, widest at the middle, 5-7 mm long, 3-4 mm thick, sessile, slightly flattened on the ventral surface, rounded on the dorsal surface, cymes about 5 cm broad, somewhat less high, with a few lanceolate, pale green bracts, flowers not sessile, petals spreading in anthesis, twice as long as the sepals, distinct, yellow, lanceolate, acuminate, 6-7 mm long, 1 5-2 mm wide, sepals lanceolate, pale green, fleshy, especially near the apex, obtuse, striate, stamens two-thirds as long as the petals, follicles erect, 4-5 mm long with spreading styles

Perenne, caulibus erectis glabris 10-20 cm altis, foliis ellipsoidalibus vel ovoidalibus glaucis 5-7 mm longis 3-4 mm crassis, cymis 5 cm latis, petalis flavis lanceolatis 6-7 mm longis, sepalis lanceolatis viridibus obtusis, folliculis erectis 4-5 mm longis

WASHINGTON north and northwest slopes at elevations of 2500 ft to 3000 ft Peshastin Creek Wenatchee Mountains, Chelan Co, (type locality), *E J Newcomer,* November, 1928, Bear Gap, on the boundary between Yakima and Pierce counties, elevation about 6000 ft *E J Newcomer,* August 16 1930

Specimens of this Sedum from the type locality were communicated to the writer by Mr Elias Nelson of Yakima, Washington, under his collection number 1679 (type in Herb State College of Washington) Mr Nelson, in a letter dated June 14, 1930, states, " no 1679 was brought to me by E J Newcomer of Yakima in November, 1928 from Peshastin Creek in the Wenatchee Mountains It grew on north and northwest slopes at elevations of 2500 to 3000 ft Both Mr Newcomer and I have grown it in our rockeries since then " Mr Newcomer sent the specimens from Bear Gap to the writer in September, 1930 He reports that this new Sedum is fairly common along the ridge of the Cascade Mountains in this locality, growing with *S divergens* Although the plants had been collected a month before, when planted at Pullman they quickly revived, and are growing vigorously in the College greenhouse at the present time Specimens received from Mr Nelson earlier in that year were planted in the garden of Dr F L Pickett, where they have been under observation since that time The description has been written from living plants from Mr Nelson's garden in Yakima

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* Contribution No 38 from the Department of Botany State College of Washington.

This new Sedum is apparently somewhat closely related to *S spathulifolium* Hook and to *S stenopetalum* Pursh The former species has spatulate, obtuse, flat leaves, the leaves of the latter are linear-oblong, acute, not glaucous From *S oreganum* Nutt, *S rupicolum* differs in having the petals distinct *S divergens* Wats, *S Douglasii* Hook, and *S Leibergii* Britt differ by having the carpels, and later the follicles divergent As Mr Nelson has pointed out, a very striking characteristic of this species is that the leaves fall away from the stem at the slightest touch In this respect it resembles the cultivated *S dasyphyllum* L

PENSTEMON amabilis n sp Plants perennial, glabrous, except the slightly glandular-puberulent inflorescence, stems several, tufted, slender, erect, simple, 15-20 cm high, from a short, stout, woody caudex, basal leaves numerous, tufted, long petioled, firm, elliptic or ovate, finely and regularly serrate, acute, cuneate at base and gradually tapering into the petiole, 2-4 cm long, petioles 1 5-4 cm long, cauline leaves opposite, lanceolate, serrulate above the middle, sessile and somewhat clasping, acuminate, 2-2 5 cm long, thyrsus narrow, composed of 3-5 fascicles, pedicels filiform, 2-3 mm long, sepals 3-4 mm long, ovate-lanceolate, acuminate, viscid-puberulent, broadly scarious margined below the apex and somewhat erose, corolla 10-13 mm long, blue, externally glandular-puberulent, glabrous within, tube almost cylindrical or slightly wider upward, anther sacs bluish, dehiscent from base to apex, explanate in age, 1 mm long, glabrous, sterile filament densely bearded near apex with yellowish hairs, fertile filaments glabrous, capsuule not seen

Perennis, glaber praeter inflorescentiam glanduloso-puberulam, basi fruticulosa, foliis radicalibus petiolatis elliptico-ovatis serratis, caulinis lanceolatis amplexicaulibus serrulatis, thyrso angusto, calyce segmentis ovato-lanceolatis, lanceolatis acuminatis glanduloso-puberulis, margine segmentorum membranaceo, corolla 10-13 mm longa caerulea cylindricosa intus glabra extus glanduloso-puberula, antheris glabris cum loculis primum distinctis denum divaricatis a basi ad apicem dehiscentibus, filamentis sterilibus barbatis, capsua ignota

WASHINGTON on partly wooded slopes Blewett Pass Kittitas Co, June 23 1930, *Elias Nelson* 1682 (type in Herb State College of Washington)

Penstemon amabilis would be placed in the subgenus Eupenstemon, section Graciles, according to a revision of some Rocky Mountain species by Dr Pennell[1] It is apparently most nearly related to *P virens* Pennell, and to *P gracilis* Nutt *P virens* is known to occur only in Wyoming and Colorado According to Dr Pennell, *P gracilis* ranges "in north-central Wyoming and eastern Colorado to the base of the foothills Manitoba to Saskatchewan, south probably to Kansas and northwestern New Mexico"

These three species may be distinguished as follows *P gracilis* has the stems glabrous, the stem-leaves linear-lanceolate or linear, the calyx-lobes elongate-lanceolate, not or scarcely scarious margined, and the corolla 18-20 mm long, lilac or whitish, slightly bearded within In *P virens* the stems are puberulent in lines, the stem-leaves lanceolate, the calyx-lobes ovate-lanceolate, scarious margined and the corolla is 15-18 mm long, light blue, pubescent within *P amabilis* has the stems glabrous, the stem-leaves lanceolate, the calyx lobes ovate-lanceolate with scarious margins, and the corolla 10-13 mm long, dark blue, glabrous within

PENSTEMON ATTENUATUS Dougl, var **glabratus** n var Specimens of this plant were collected in June, 1927 in moist, grassy meadows near Benewah, Benewah Co, Idaho It was found later that the late Dr C V Piper had collected similar plants in July, 1898 in wet meadows at Collins, which is about twenty-five miles southeast of Benewah, in Latah County Dr Piper had labelled his plants "*Penstemon attenuatus Dougl ?*" This variety differs from the species in having the inflorescence glabrous instead of viscid-pubescent

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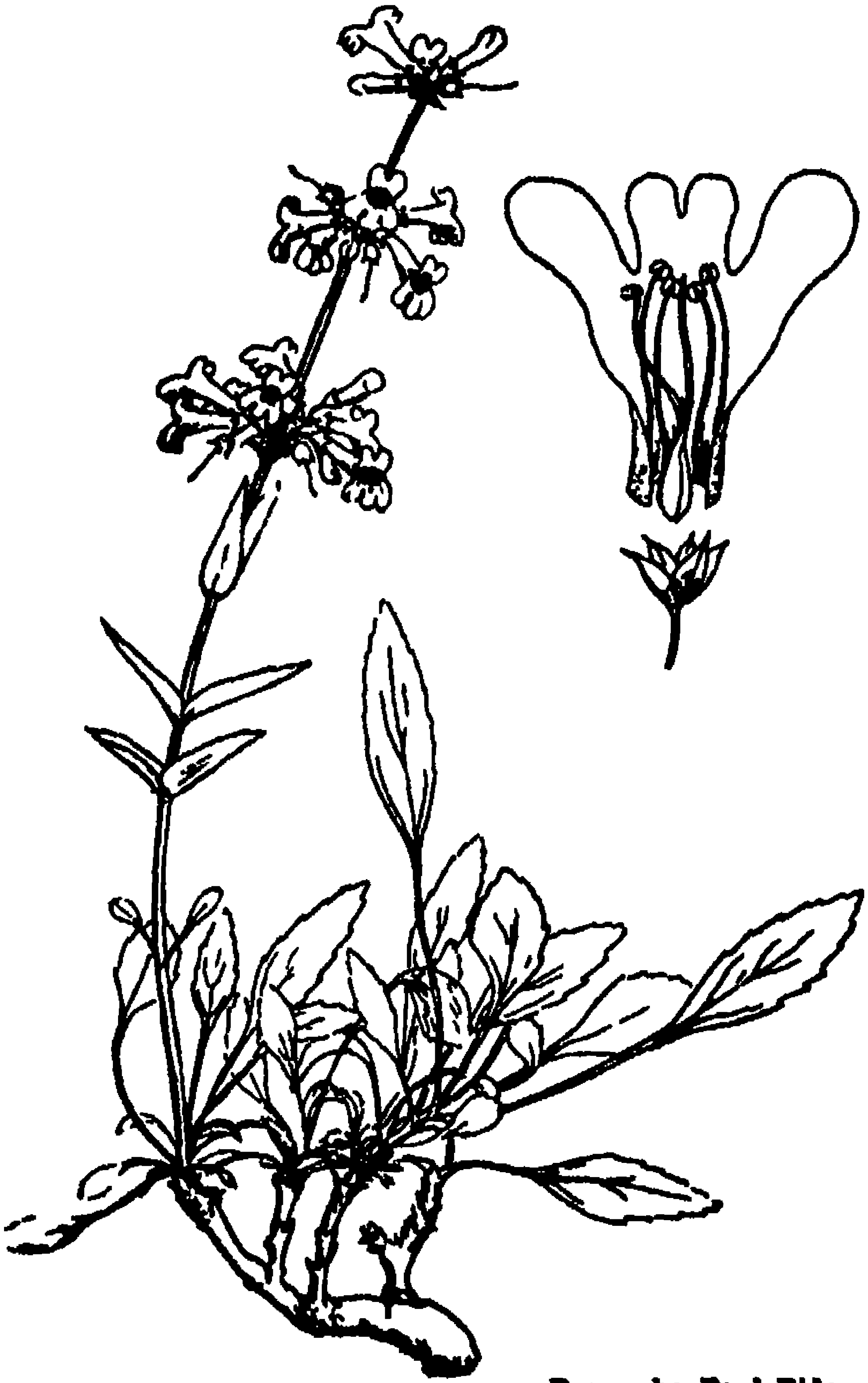
[1] Contr U S Nat Herb 20 325 381 1920



—Drawn by Paul Eide

Penstemon amabilis x ½ lower lip spread open and calyx x 2

A specie differt in inflorescentia glabra

IDAHO Collins, Latah Co, *C V Piper,* July, 1898, Alder Creek, near Benewah, Benewah County, June 19, 1927, *G N Jones* 679 (type in Herb State College of Washington)

CENTAUREA IBERICA Trev The addition of this adventive species to the flora of Washington makes a total of seven members of this genus, all of which are weeds, to occur within the state It is a native of Asia Minor, and, according to Mr C A Weatherby of the Gray Herbarium of Harvard University, who determined the following collection, the only previous North American record of this plant is from California.

WASHINGTON cultivated land, Ellensburg Kittitas Co, August 15, 1929, *Dr A L Hafenrichter*

LESSING AND ENGLISH DOMESTIC TRAGEDY

PAUL P KIES

This paper is a consideration of Lessing's relation to English tragedy during the first nine years of his dramatic career The main contention is that, contrary to the common assumption, the noted German playwright was well read in English domestic tragedy at the time of writing *Miss Sara Sampson* (1755)

In the "Abhandlungen von dem weinerlichen oder ruhrenden Lustspiele" (1754), Lessing recognizes two main kinds of tragedy The traditional type deals with kings and other persons of high rank, middle-class tragedy *(burgerliches Trauerspiel)*—usually called "domestic tragedy" in English—takes its leading characters from the middle classes This distinction is stated in the following sentence

> Hier [i e in tragedy] hielt man es fur unbillig dass nur Regenten und hohe Standespersonen in uns Schrecken und Mitleiden erwecken sollten, man suchte sich also aus dem Mittelstande Helden und schmallte ihnen den tragischen Stiefel an[1]

In a letter to Friedrich Nicolai dated January 21, 1758, he implies further that middle-class tragedy is concerned with domestic situations rather than with political interests He says concerning his plan of changing the old Roman story of Virginia into a domestic tragedy (speaking of himself in the third person)

> Sein jetziges Sujet ist eine bürgerliche Virginia, der er den Titel *Emilia Galotti* gegeben Er hat nehmlich die Geschichte der römischen Virginia von allem dem abgesondert was sie fur den ganzen Staat interessant machte, er hat geglaubt dass das Schicksal einer Tochter die von ihrem Vater umgebracht wird, dem ihre Tugend werther ist, als ihr Leben, fur sich schon tragisch genug, und fahig sey die ganze Seele zu erschuttern wenn auch gleich kein Umsturz der ganzen Staatsverfassung darauf folgte[2]

One of Lessing's important innovations was the introduction of domestic tragedy into Germany The only German *burgerliches Trauerspiel* before 1755 is the seventeenth-century *Cardenio und Celinde* of

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[1] Lachmann Muncker VI 6 Lachmann Muncker'' is used in this paper to designate the following edition of Lessing s works Gotthold Ephraim Lessings sämmtliche Schriften, originally edited by Karl Lachmann, 3rd (rev) ed by Franz Muncker Stuttgart, 1886 ff

[2] Lachmann Muncker XVII 133

Gryphius, a work practically unknown to the German literary public of Lessing's day Criticism had frowned upon the use of middle or lower class characters as tragic heroes Martin Opitz in his famous *Buch von der deutschen Poeterei* (1624) stated that the majesty of tragedy required personages of elevated rank

> Die Tragedie ist an der maiestet dem Heroischen getichte gemesse, ohne das sie selten leidet das man geringen standes personen und schlechte sachen einführe[3]

Gottsched, literary dictator in Germany immediately preceding Lessing's career, held the same opinion

> Die Tragödie ist von der Comodie nur in der besondern Absicht unterschieden, dass sie an statt des Gelachters die Verwunderung, das Schrecken und Mitleiden zu erwecken suchet Daher pflegt sie sich lauter vornehmer Personen zu bedienen die durch ihren Stand Nahmen und Aufzug mehr in die Augen fallen, und durch grosse Laster und traurige Unglucks Falle solche hefftige Gemuths Bewegungen erwecken konnen[4]

Lessing began his experiments in tragedy with the traditional type For instance, the fragmentary *Giangir, oder der verschmahte Thron* (April 17, 1748), his first original attempt, treats the well-known story of Mustapha and Zanger (Zeangir)

No conclusive evidence that Lessing studied English tragedy before 1749 has yet been cited[5] In 1749, however, he read Otway, and before many years had elapsed he was acquainted with the other leading Restoration writers of tragedy—Lee, Dryden, and Southerne

Lessing's *Samuel Henzi* (1749), a dramatization of a conspiracy at Bern in 1749, was influenced by Otway's *Venice Preserved*, *or, A*

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[3] Reprint of original edition ed W Braune (Halle 1882) p 22

[4] Johann Christoph Gottsched Versuch einer kritischen Dichtkunst, Leipzig 1730 p 136 A review written by Lessing himself says concerning *Miss Sara Sampson* Ein bürgerliches Trauerspiel! Mein Gott! Findet man in Gottscheds critischer Dichtkunst ein Wort von so einem Dinge? *Berlinische Privilegirte Zeitung* Berlin May 3 1755 (Lachmann Muncker VII, 26)

[5] Arnold Lehmann in his *Das Schicksal Mustapha s des Sohnes Solyman's II in Geschichte und Literatur* (Mannheim, 1908) pp 97 98 thinks that *Giangir* (1748) was inspired by David Mallet's *Mustapha* (1739) Though such may have been the case, the evidence presented is not very strong Lessing s Leben des Herrn Jacob Thomson' (1754) contains nothing about Mallet not to be found in the avowed source the biography of Thomson in Cibber s *The Lives of the Poets of Great Britain and Ireland* (London 1753), V 194 ff Contrary to the belief that has recently been gaining currency Mallet's play does not use the *Phaedra* motif the feature in which Lessing s plot differs from the historical accounts and the other dramatic versions

Plot Discovered (1682)[6] That the dramatist knew of *Venice Preserved* in 1749 as a tragedy dealing with a conspiracy is indicated by the fact that it is discussed in Voltaire's *Lettres philosophiques,* Nos 18 and 19, published by Lessing and Mylius in the *Beitrage zur Historie und Aufnahme des Theaters*[7] Though the *Beitrage* were not issued till 1750, the "Vorrede" is dated October 1749

The way in which Wernier becomes associated with Henzi's men was obviously suggested by the manner in which Jaffeir in the English tragedy joins the conspiracy Specific points of resemblance are Henzi (Pierre) meets his friend Wernier (Jaffeir), they complain of the tyranny of the *Rath*, Henzi reveals his connection with the conspiracy, the conspirators, who have met without Henzi, quarrel, Henzi arrives and says that he has confided the secret to a friend, the conspirators think they are betrayed, Wernier enters, the conspirators accept him and embrace him Lessing implies that he added this material to the Henzi story

> Es liegt wenig oder nichts daran ob die Entdeckung wirklich sozugegangen, und ob Wernier erst an dem Tage der Entdeckung an dem Geheimnisse Theil genommen genug dass beydes seyn konnte und die Hauptsache nichts darunter leidet[8]

Lessing read widely in Otway He made notes on the *Soldier's Fortune* in 1756[9] In the scenario *Alcibiades,* assigned by Muncker to about 1760-65,[10] he cited Otway's tragedy of the same title[11] In the *Hamburgische Dramaturgie,* No 15 (June 19, 1767), he included Otway in a list of six representative English writers of poetic tragedy in such a way as to imply that he was familiar with Otway's blank verse tragedies *(Caius Marius, The Orphan, Venice Preserved)*, after commenting on the rhymed couplets that end the acts of Hill's English translation of Voltaire's *Zaïre,* he says

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[6] This connection was pointed out by Hermann Hettner *Geschichte der deutschen Literatur im achtzehnten Jahrhundert,* 4th ed (Braunschweig 1893 94) II 455 Hettner s conclusion has been accepted in Josef Caro s "Lessing und die Engländer" *Euphorion,* VI 474 and in Schmidt s *Lessing,* 4th ed (Berlin, 1923) I 210

[7] *Beiträge* (Stuttgart 1750) p 96

[8] Lachmann Muncker V 111

[9] Lachmann Muncker XIV 197

[10] Lachmann Muncker III, 'Vorrede,'' p xii

[11] Lachmann Muncker III, 401 02

> Vergleichungen enthalten sie freylich nicht aber, wie gesagt, unter allen dergleichen gereimten Zeilen mit welchen Shakespear und Johnson, und Dryden, und Lee, und Otway und Rowe und wie sie alle heissen ihre Aufzuge schliessen sind sicherlich hundert gegen funfe die gleichfalls keine enthalten"[22]

As has been frequently pointed out, *Henzi* departs from the lofty tone of French neo-classic tragedy It contains common citizens as the leading characters and treats a contemporary event[23] A writer in the *Neue Erweiterungen* (1755) even called it a *burgerliches Trauerspiel*[24] In these innovations, especially in the former, *Venice Perserved* evidently exerted an important influence, though the young dramatist may also have read at this time some domestic tragedies, such as Otway's *The Orphan* (1680) and Rowe's *The Fair Penitent* (1703)

The second Restoration writer of tragedy coming under consideration here is Nathaniel Lee As I have shown elsewhere, this dramatist's *Lucius Junius Brutus* was the basis of Lessing's *Das befreite Rom,* a scenario evidently written before 1755—probably not long after 1749[25] Like *Henzi* (though in a different way), *Das befreite Rom* violates the tradition of French neo-classical tragedy "Die Pobelscenen und die 'Possen' des Brutus," says Danzel, "hatte Lessing wenigstens nicht den Franzosen abgelernt"[26] These features are to be found in *Lucius Junius Brutus*

In a letter to Moses Mendelssohn December 18, 1756, Lessing asked for the volume of Cibber's *The Lives of the Poets of Great Britain and Ireland* containing the biography of John Dryden[27] The German author must have been acquainted with works of Dryden for some time before the date of the letter, inasmuch as he was preparing an article on the British playwright for the *Theatralische Bibliothek* (1754-58) In the "Geschichte der englischen Schaubuhne" (1758) he inserted "Johann Dryden Von diesem und seinen sammtlichen dramatischen

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[22] Lachmann Muncker IX, 247

[23] Cf Danzel and Guhrauer Gotthold Ephraim Lessing, 2nd ed (Berlin 1880) I 165 Caro op cit., p 478 Waldemar Oehlke Lessing und seine Zeit (Munich 1919) I 374

[24] Cf Danzel and Guhrauer op cit., pp 165 66

[25] 'Lessing and Lee,' Journal of English and Germanic Philology, XXVIII 402 09 I wish to add that Voltaire s Brutus is precluded as a source of Das befreite Rom, inasmuch as it deals with a different motif the treachery of Brutus sons

[26] Danzel and Guhrauer, op cit., I 166 n 2

[27] Lachmann-Muncker XVII, 86

Werken werde ich in dem folgenden XIIIten Artikel umstandlich zu handeln anfangen "[18] In the thirteenth article—entitled "Von Johann Dryden und dessen dramatischen Werken" (1758)—he published an abridged translation of Dryden's *Essay of Dramatic Poesie,* intending to discuss the plays in a subsequent article This *Essay* helped to lead Lessing to recognize the greatness of Shakespeare In 1763 Lessing spoke of ordering a copy of Dryden directly from England,[19] in 1767 he praised Dryden's epilogues[20] and included him in a list of six representative English writers of blank verse tragedies (the list referred to above in connection with Otway),[21] and in 1776 he sent a copy of Dryden to J J Eschenberg[22]

The interest in Dryden manifested in a review of a biography of the Restoration neo-classicist on May 26, 1753[23] and in the "Leben des Herrn Philipp Nericault Destouches" (1754)[24] suggests that Lessing was familiar with the works of Dryden in 1753-54 In fact, he probably read plays of this English dramatist as early as 1749 or 1750 In Voltaire's *Lettres philosophiques,* Nos 18 and 19, Dryden is classed as one of the three leading English writers of tragedy, the other two being Shakespeare and Addison We have evidence that in 1749 Lessing was familiar with all five authors discussed by Voltaire as the outstanding English writers of comedy—Wycherley,[25] Congreve,[26] Vanbrugh,[27] Cibber, and Steele[28] Moreover, as was pointed out above, the young German dramatist by the end of 1749 knew Otway's *Venice Preserved,* a tragedy severely criticized by Voltaire In a footnote to Mylius' German translation of the two *Lettres* in the *Beitrage zur Historie und Aufnahme des Theaters* (1750), great confidence in Voltaire's judgment concerning English drama is expressed "Weil der Herr von Voltaire beynahe der einzige ist, der unter seinen Landsleuten unparteyisch und vortheilhaft von der Schaubuhne der Englander geurtheilet hat, so haben wir fur billig gehalten seiner Urtheile und Nachrichten davon uns zuerst zu bedienen "[59] Lessing himself, in the list of six representative English dramatists in the "Vorrede" (dated October 1749) to the *Beitrage,* mentioned only Shakespeare and Dryden as exponents of tragedy (including also four of Voltaire's five outstanding English comedy writers—Wycherley, Congreve, Vanbrugh, and Cibber) [60] In view of Lessing's great interest in English drama at the time,[61] the probability is strong that he made an early effort to obtain works of the three men mentioned bv Voltaire as famous English tragedians—Shakespeare,[62] Dryden, and Addison—provided that he was not already familiar with them on becoming acquainted with the *Lettres*

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[18] Lachmann Muncker VI 249 n 1

[19] Lachmann Muncker XVII 194

[20] Lachmann Muncker IX 213

[21] Lachmann Muncker IX 247

[22] Lachmann Muncker XVIII 216

[23] Lachmann Muncker V 169

[24] Lachmann Muncker VI 157

[25] Cf my Lessing's Early Study of English Drama,' Journal of English and Germanic Philology, XXVIII 16 17

[26] Ibid., pp 24 29

[27] Cf. my The Sources of Lessing's Die Juden, Philological Quarterly, VI 406-07

[28] The evidence in regard to Cibber and Steele will be presented in a forthcoming article.

Lessing knew of at least one tragedy of Thomas Southerne by 1751, inasmuch as he reviewed in that year a French edition of an abstract from *Oroonoko* (1696) [63]

Two English neo-classicists of the early eighteenth century that Lessing read before 1755 are Joseph Addison (1672-1719) and James Thomson (1700-1748) As was pointed out above, Lessing was probably familiar with the dramatic work of Addison by 1750 This conclusion is particularly plausible because of the fact that the famous essayist's *Cato* (1713) was a great favorite of Gottsched, German literary dictator in the second quarter of the eighteenth century In 1753 our young author and critic reviewed Frau Gottsched's German translation of this tragedy[64] In the *17th Literaturbrief* (1759) Lessing insisted that Gottsched had greatly overestimated the merit of Addison's *Cato* [65]

Thomson's neo-classical tragedies greatly fascinated Lessing in the early 1750's In 1754 the German writer published an article on Thomson ("Leben des Herrn Jacob Thomson") in the *Theatralische Biblio-*

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[59] Stuttgart 1750 p 96

[60] Lachmann Muncker, IV 52

[61] Cf Lessing's Early Study of English Drama The Sources of Lessing s Die Juden,' and the forthcoming article on Lessing s Relation to Early English Sentimental Comedy '

[62] Definite evidence however that Lessing read Shakespeare in the original before the late 1750's is lacking

[63] Lachmann Muncker IV 261

[64] Lachmann Muncker V 168 69

[65] Lachmann Muncker VIII 42 For other references to Addison see Lachmann Muncker, VI, 156 57, IX, 254

thek, specifying as his source Cibber's *The Lives of the Poets of Great Britain and Ireland* In this article he stated that he had previously worked on a translation of Thomson's *Agamemnon*[56] This prose translation—found in the Breslau papers (together with a fragmentary translation of *Tancred and Sigismunda*)—extends into the fifth scene of Act II In 1756 in a preface to a German prose translation of Thomson's tragedies Lessing praised the Englishman very highly[57]

Thus far we have considered six Restoration and early eighteenth century English writers of tragedy—Otway, Lee, Dryden, Southerne, Addison, Thomson We have also observed that in *Henzi* and *Das befreite Rom* Lessing departed from the tradition of French neo-classicism to the extent of employing middle-class heroes in tragedy, treating a contemporary event, presenting a mob on the stage, and admitting "Possen" into tragedy But he was to be guilty of still greater heresy against the school of Gottsched In his epoch-making domestic tragedy—*Miss Sara Sampson* (1755)—he treated a domestic situation, disregarded the rule of the unity of place and used prose dialogue

Lessing's interest in domestic tragedy, as is well known, was inspired primarily by English drama In the "Abhandlungen von dem weinerlichen oder ruhrenden Lustpiele" (1754), he stated that middle-class tragedy had originated in England, and in *Miss Sara Sampson* he used only English characters and scenes

As early as 1750—probably earlier—Lessing was aware of the existence of middle-class tragedy as a dramatic genre The term *burgerliches Trauerspiel* is used in the "Theatralische Neuigkeiten aus Paris" in the *Beitrage zur Historie und Aufnahme des Theaters* (1750)[58] These "Neuigkeiten"—taken from *La Bigarure*, a French periodical published at The Hague[59]—were evidently prepared by Lessing himself, inasmuch as the same fondness for the paradox "Tragedie pour rire, ou Comedie pour pleurer" is displayed[illegible] as in his *Die Juden*[illegible] (1749) and in a footnote to his translation (1750) of Plautus' *Captivi*[illegible] But even if he should not have been responsible for the insertion of the Paris news item in the *Beitrage*, we may safely assume that, as joint editor of the magazine, he at least read the whole content of the first issue

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[56] Lachmann Muncker VI 66

[57] Lachmann Muncker VII 66 71

[58] An item concerning Voltaire s Nanine, a middle-class comedy reads Der tragische Inhalt dieses Stücks hat bey jedermann den meisten Beyfall erhalten Dieses ist auch nicht zu verwundern da dieses allemal die Stärke des Herrn von Voltäre gewesen Das Komische hingegen ist unter dem Mittelmässigen und ganz matt Es ist ein blosses Gespräch ohne Stärke ohne Salz ohne Natur ohne Annehmlichkeit und überhaupt ist die Materie mehr zu einem bürgerlichen Trauerspiele als zu einer guten Tragikomödie geschickt'' (Stuttgart 1750 p 288)

[59] That these Neuigkeiten'' were taken *from* La Bigarure is evident from a comparison of the first installment (ibid., *pp* 110-22) with a review (probably by Mylius or Lessing) of La Bigarure in the Berlinische Privilegirte Zeitung, Nov 6 1749 (Lachmann-Muncker, IV, 39 40)

Lessing probably became acquainted with English domestic tragedy rather early in his career Examples of the species had presumably come to his attention before 1753 through his extensive reading of English drama during the previous six years The leading English writers of domestic tragedy from 1660 to 1755—Otway, Southerne, Centlivre, Rowe, Hill, Lillo, Charles Johnson, Moore—produced also plays of other types As has already been suggested, he may have become familiar with one or more domestic tragedies as early as 1749

By 1755 Lessing was well read in English domestic tragedy A remark in the "Abhandlungen von dem weinerlichen oder ruhrenden Lustspiele" indicates that by 1754 he had already given considerable thought and attention to the subject of domestic tragedy

> Das erstere [i e Lustspiel] hat man um einige Staffeln erhöhet, und das andre [i e Trauerspiel] um einige herabgesetzt Dort glaubte man dass die Welt lange genug in dem Lustspiele gelacht und abgeschmackte Laster ausgezischt habe, man kam also auf den Einfall, die Welt endlich einmal auch darinne weinen und an stillen tugenden ein edles Vergnugen finden zu lassen Hier hielt man es fur unbillig das nur Regenten und hohe Standespersonen in uns Schrecken und Mitleiden erwecken sollten man suchte sich also aus dem Mittelstande Helden, und schnallte ihnen den tragischen Stiefel an
>
> Die erste Veranderung brachte dasjenige hervor, was seine Anhänger das rührende Lustspiel, und seine Widersacher das weinerliche nennen
>
> Aus der zweyten Veranderung entstand das burgerliche Trauerspiel
>
> Jene ist von den Franzosen und diese von den Engländern gemacht worden Ich wollte fast sagen, dass sie beyde aus dem besondern Naturelle dieser Völker entsprungen zu seyn scheinen Der Franzose ist ein Geschöpf, das immer grosser scheinen will, als es ist Der Englander ist ein anders, welches alles Grosse zu sich hernieder ziehen will Dem einen ward es verdrusslich, sich immer auf der lächerlichen Seite vorgestellt zu sehen, ein heimlicher Ehrgeitz

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[illegible] Stuttgart, 1750 p 123

[illegible] Sc X, Lachmann Muncker I 392

[illegible] Lachmann Muncker IV 87

trieb ihn, seines gleichen aus einem edeln Gesichtspunckte zu zeigen Dem andern war es argerlich gekronten Hauptern viel voraus zu lassen, er glaubte bey sich zu fuhlen, dass gewaltsame Leidenschaften und erhabne Gedanken nicht mehr fur sie, als fur einen aus seinen Mitteln waren

Dieses ist vielleicht nur ein leerer Gedanke, aber genug, dass es doch wenigstens ein Gedanke ist -Ich will fur diesesmal nur die erste Veranderung zu dem Gegenstande meiner Betrachtungen machen, und die Beurtheilung der zweyten auf einen andern Ort sparen[63]

This extract indicates that Lessing had a keen interest in English domestic tragedy before October 17, 1754, the date on which his own review of the first number of the *Theatralische Bibliothek* appeared in the *Berlinische Privilegirte Zeitung*[64] The fact that the comment on middle-class tragedy was made incidentally in a discussion on middle-class comedy implies that this interest was not new at the time of the preparation of the "Abhandlungen von dem weinerlichen oder ruhrenden Lustpiele" Moreover, Lessing himself stated that he had been collecting material for the *Theatralische Bibliothek* (1754) ever since the discontinuance of the *Beitrage zur Historie und Aufnahme des Theaters* in 1750[65], and the "Abhandlungen," which was run as the first article in the first issue, may have been prepared a considerable length of time before its publication As has already been suggested, Lessing had probably become interested in domestic tragedy by 1753 or earlier But even if his attention was not directed toward the new type of play till the middle of July 1754, three months before the appearance of the "Abhandlungen" in print, he still had more than six months before going to Potsdam to write *Miss Sara Sampson* During that interval he could easily have obtained copies of domestic tragedies directly from England if they were not available to him in Germany

The tone of the passage quoted above not only indicates a great interest in English domestic tragedy, but also implies considerable familiarity with it No doubt the interest itself was primarily the result of the actual reading of the plays The term *die Englander* suggests that Lessing was referring to a group of writers rather than to perhaps two individuals One would not expect a scholarly man like him to put into print a theory concerning the *raison d'etre* of English domestic tragedy unless he was acquainted with more than one or two examples Neither would one suppose that he would announce his intention of writing a treatise on domestic tragedy if he did not already have a reasonable knowledge of the subject At any rate, the very announcement indicates such a keen interest in the topic that if he did not already possess considerable information, he would probably make an immediate effort to secure additional specimens of the dramatic type in question In July 1756 he offered to send Friedrich Nicolai copious notes which he had prepared on the subject of domestic tragedy, although he did not fulfill his promise[46] If Lessing made as thorough a study of English domestic tragedy as he had made of the English schools of the other dramatic types—Restoration comedy,[47] sentimental comedy,[48] and Restoration and early eighteenth-century non-domestic tragedy[49]—he was probably familiar with eight or more examples by the beginning of 1755

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[63] In Theatralische Bibliothek, Erstes Stück (Berlin, 1754), Lachmann Muncker, VI 6 7

[64] Lachmann Muncker V, 437

[65] Lachmann Muncker, VI, 4

Two domestic tragedies known to Lessing at the time of the production of *Miss Sara Sampson* (1755) are Charles Johnson's *Caelia* (1733) and Mrs Susanna Centlivre's *The Perjur'd Husband* (1700) These pieces, as I have shown elsewhere, have plot connections with the German play[50]

Lessing seems also to have been familiar with Thomas Cooke's *The Mournful Nuptials, or, Love the Cure of All Woes* (1739)—published in 1744 in three-act form as *Love the Cause and Cure of Grief, or the Innocent Murderer* *Der Misogyn* (1748), based chiefly on Lansdowne's *The She-Gallants,*[51] contains an episode not to be found in its main source Leander loves Laura, but, because her father has brought a lawsuit against him, fears to ask for her hand Finally the young man settles the suit by voluntarily paying the whole consideration, whereupon Wumshater consents to the marriage of the lovers At the beginning of *The Mournful Nuptials,* the situation is substantially the same, the chief difference being that the girl's father sues the lover's father instead of the lover himself The Leander episode does not have an integral connection with the remainder of Lessing's comedy, for Laura could fall in love with the she-gallant without having another lover Hence this motif could have been added at any time previous to early 1755, the date of the first publication of *Der Misogyn* That it was added in 1754 or early 1755—the period during which Lessing was intensely interested in domestic tragedy—is highly plausible, inasmuch as *Der Misogyn* seems to have been retouched at that time[32] A special "point of contact" for the association of *The Mournful Nuptials* with *Der Misogyn* is in the fact that in both plays the girl's father is a gruff, stubborn man

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[46] On June 20 1756 he wrote to Friedrich Nicolai Ich habe eine Menge unordentlicher Gedanken uber das bürgerliche Trauerspiel aufgesetzt die Sie vielleicht zu der bewussten Abhandlung brauchen können wenn Sie sie vorher noch ein Wenig durchgedacht haben (Lachmann Muncker XVII, 59)

[47] JEGP, XXVIII 16 34 and PQ VI 406 10

[48] The evidence is to be presented in a forthcoming article

[49] See above

[50] "The Sources and Basic Model of Lessing's Miss Sara Sampson," Modern Philology, XXIV, 65 90

[51] JEGP, XXVIII, 32 34

Der Schlaftrunk (1766-68), on which Lessing worked at about the time of enlarging *Der Misogyn* for the 1767 edition of his comedies, likewise deals with a lawsuit that threatens the union of two lovers In the first plan of this fragment, as in *The Mournful Nuptials,* the suit is between the fathers of the young people The final version, though differing greatly from the first, still contains the character of the headstrong man That *Der Schlaftrunk* should be connected with a tragedy is particularly plausible in view of the following statement of Lessing's brother Karl

> In einer Gesellschaft guter Freunde, wo er [i e the dramatist] und Herr Professor Rammler auch waren, kam die Rede auf die Stoffe, welche zu einer Komodie am besten passten Mein Bruder behauptete, man konne aus allem eine Komödie oder Tragodie machen indem es mehr auf die Bearbeitung des Stoffs als auf den Stoff selbst ankame Der Stoff ware nur arm, wenn es der Dichter ware Dieses schien der Gesellschaft etwas paradox, und Herr Professor Rammler fragte ihn ob er es selbst mit der That beweisen wollte Warum nicht erwiederte mein Bruder Nun so machen Sie versetzte jener ein Lustspiel, wo ein Schlaftrunk die Katastrophe ist, und benennen es darnach Die ganze Gesellschaft billigte es einmuthiglich und mein Bruder versprachs[33]

In the case of *Miss Sara Sampson* (1755)—in which material from a comedy was used as the basis of a tragedy[34]—the process was reversed

We may take for granted that at the time of producing his own domestic tragedy the dramatist was acquainted with Otway's *The Or-*

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[32] Lachmann Muncker V 271

[33] Lachmann Muncker, III 414 n 1

[34] Cf MP, XXIV 66 78

phan (1680), Rowe's *The Fair Penitent* (1703), Lillo's *The London Merchant* (1731), Moore's *The Gamester* (1753), and Hill's *The Fatal Extravagance* (1720) As for *The Orphan,* mention has already been made of the facts that Lessing read at least three other plays by the same author, and that a passage in the *Hamburgische Dramaturgie,* No 15, implies that in 1767 he knew all of Otway's blank verse tragedies *(Caius Marius, The Orphan, Venice Preserved)* Such a famous Restoration play as *The Orphan* would not be unknown to him in 1755 As was suggested above, this piece presumably was one of the first domestic tragedies read by the German dramatist, inasmuch as he studied another tragedy *(Venice Preserved)* by Otway in 1749 Because of not being an extreme form of domestic tragedy, *The Orphan* would serve as a gradual transition from the older type of tragedy to the newer

The Fair Penitent (1703), as is implied by the passage from the *Hamburgische Dramaturgie* just referred to,[85] was known to Lessing before June 19, 1767 The context indicates that at the time of writing the passage he had a good knowledge of Rowe's plays He had evidently read them before 1759, for in the *Literaturbriefe,* Nos 63 and 64 (1759), he charged that Wieland's *Lady Johanna Gray* (1758) contains passages plagiarized from Rowe's *Jane Gray,*[86] and praised Rowe as "einen der grossten englischen Dichter"[87] That the dramatist became acquainted with *The Fair Penitent* before 1755 (probably as early as 1750 or 1751) is almost a certainty, inasmuch as it was one of the most popular of the Restoration and early eighteenth-century English tragedies[88]

The London Merchant was so well known in England at Lessing's time that it would almost certainly come to his attention if, after becoming interested in domestic tragedy, he sought examples of the species One should bear in mind, however, that there is no actual proof of his knowledge of Lillo's drama before the production of *Miss*

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[85] Lachmann Muncker, IX 247

[86] Lachmann Muncker VIII 170 78

[87] Lachmann Muncker VIII 173

[88] Cf A T Bartholomew in The Cambridge History of English Literature (Cambridge Eng 1907 ff) VIII 221 22 The Fair Penitent proved one of the most popular plays of its time. It was constantly before the public till 1825, or thereabouts No play was more popular in the eighteenth century

Sara Sampson (1755) The two references cited by Josef Caro[59]—one in Lessing's "Vorrede" to a German translation of James Thomson's tragedies[60] and the other in a letter to Moses Mendelssohn on December 18, 1756[61]—have no weight, for they were both written in 1756 By that time *The London Merchant* had become well known in Germany It had been performed in several German cities in 1755 and had been published in a German translation based on the original[62] These performances and this translation, however, would have been too late to introduce Lessing to *The London Merchant* before he began *Miss Sara Sampson* He went to Potsdam in January 1755 to write his play,[63] and he had presumably planned it before that time Furthermore, as I shall point out in another place, the parallelisms between *The London Merchant* and *Miss Sara Sampson* which have been cited by Danzel[64] and Albrecht[65] are not conclusive evidence that Lessing consulted the Lillo work while preparing his own domestic tragedy

Three domestic tragedies—Moore's *The Gamester,* Hill's *The Fatal Extravagance,* and the anonymous *A Yorkshire Tragedy*—are mentioned by Lessing in an undated note in the *Kollektaneen* "*Edward Moore* Der Verfasser des Spielers Ich kann zeigen, dass dieses Stuck aus Hills *Fatal Extravagance* und beide aus der *Yorkshire-Tragedy* genommen ist [sic]"[66] The reference is to an item in the February, 1753 issue of the *Monthly Review,* in which the statement is made that Moore's *The Gamester* is based on a story of the same name translated from the Italian The words "zu der Zeit als Moors *Spieler* herauskam (ao 1753) zu London herauskam [sic]"[67] indicate that Lessing's note was written after 1753, and therefore that the dramatist was looking through a back number of the *Monthly Review* Inasmuch as he studied back numbers of this magazine while collecting material for the

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[59] Lessing und die Engländer' Euphorion, VI 475

[60] Lachmann Muncker VII 68

[61] Lachmann Muncker XVII 86

[62] H. A. Bassewitz tr Der Kaufmann von London, oder Begebenheiten George Barnwells, Danzig, 1755

[63] Moses Mendelssohn s letter to Lessing on Februray 17 1755 indicates that the dramatist had left for the seclusion at Potsdam at least three weeks before the date of the letter (Lachmann Muncker XVII, 18 19)

[64] Danzel and Guhrauer *op cit.*, I 305 07

[65] Paul Albrecht, Lessings Plagiate (Hamburg and Leipzig 1888 91) V VI pp 1963 2483

[66] Lachmann Muncker XV 312

[67] Ibid

Hamburgische Dramaturgie[68] (1767-68), the natural inference is that the date of the note is not later than 1768 Moreover, the context indicates that Lessing was acquainted with these three domestic tragedies before he made this memorandum His remark was occasioned not by his discovery of the plot similarities among the three plays, but by the statement in the *Monthly Review* that *The Gamester* was based on the Italian story

The first of these, *The Gamester* (1753), was almost certainly known to the German dramatist as early as 1755 About 1752-54 he started a synopsis (the so-called *Ludewig und Aurora*) of another work by Moore, a stage version of an episode from Le Sage's *Gil Blas*[69] A German translation of *The Gamester*, by J J C Bode, who later went into the book business with Lessing, had been published in 1754,[70] the year before the appearance of Lessing's tragedy Inasmuch as Lessing was literary critic for an important newspaper, the *Berlinische Privilegirte Zeitung*, and was a playwright keenly interested in domestic tragedy, he would hardly fail to become acquainted with the play through this means The piece was performed on the Breslau stage October 1 of the same year[71] Perhaps he had read *The Gamester* even before this in the original English edition, which was issued in London early in 1753[72] At this time he seems to have obtained current British books soon after their publication Cibber's *The Lives of the Poets of Great Britain and Ireland*, printed in 1753, was the following year specified by him as a source for his "Leben des Herrn Jacob Thomson"[73]

The second play mentioned in the Kollektaneen passage quoted two paragraphs above is *The Fatal Extravagance* (1720) As was shown, the context implies that Lessing had become familiar with this tragedy before 1768 Additional evidence for this conclusion is to be found in a remark in the *Hamburgische Dramaturgie*, No 15 (June 19, 1767), which indicates that he had read all of Hill's plays[74] *The Fatal Extravagance* was probably known to the German dramatist before 1755 We have seen that in the year or two immediately preceding the production of *Miss Sara Sampson* he was intensely interested in the theory of domestic tragedy and even announced his intention of writing an essay on this subject No doubt he read during this period all the domestic tragedies he could obtain, and *The Fatal Extravagance* may well have been one of the number This play was advertised in the only edition of Charles Johnson's *Caelia* (London, 1733), one of the sources of *Miss Sara Sampson* (1755) Lessing could easily have obtained a copy Six editions appeared during the first eleven years, and a reprint (with Hill's name on the title page) was issued in 1753 Moreover, Lessing seems to have known Hill's translation of Voltaire's *Zaïre* in 1759 The manner in which he associates the French play with Shakespeare's *Othello* in the *17th Literaturbrief* (1759) suggests that he had read Colley Cibber's Prologue to the English version In the discussion in the *Hamburgische Dramaturgie*, No 15, he actually quotes the following lines of Cibber

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[68] Cf Lessings Werke, ed by Georg Witkowski (Leipsig and Vienna [1911?]) V 398 99

[69] The evidence for this conclusion will be presented in a forthcoming article

[70] Under the title Der Spieler Cf Jacob N Beam Die ersten deutschen Übersetzungen englischer Lustspiele im achtzehnten Jahrhundert, Hamburg and Leipsig 1906 p 55 Cf also Johann Christoph Gottsched Nöthiger Vorrath, Part II (Leipsig 1765) p 283

[71] Gottlieb Fritz Der Spieler im deutschen Drama des achtzehnten Jahrhunderts, Berlin, 1896 p 13

[72] Reviewed in the Monthly Review, Feb 1753 p 146

[73] Lachmann Muncker VI, 54

> From English Plays Zara's French author fir'd
> Confess'd his Muse beyond herself, inspir'd
> From rack'd Othello's rage, he raised his style
> And snatch'd the brand, that lights this tragic pile

Other domestic tragedies with which Lessing may have been familiar when he began work on his own are *A Yorkshire Tragedy* (1608), Thomas Southerne's *The Fatal Marriage* (1694), and Thomas Heywood's *A Woman Killed with Kindness* (1607) *A Yorkshire Tragedy*, as is shown by its being mentioned in the *Kollektanean* note already referred to, seems to have been known to him before 1768 The text was available in the 1664 and the 1685 editions of Shakespeare's works *The Fatal Marriage* may have been one of the sources of Lessing's *Der Schlaftrunk* (begun 1776) In the minor plot of this English play, as in the first plan of Lessing's comedy, the union of the lovers is brought about through a sleeping potion given to the girl's father A "point of contact" for the association of *The Fatal Marriage* with

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[74] After discussing Hill s English translation of Voltaire s Zaire, Lessing says 'Noch bis diese Stunde erscheinen in England eben so viel wo nicht noch mehr Trauerspiele, deren Akte sich mit gereimten Zeilen enden, als die es nicht thun Hill selbst hat in keinem einzigen Stücke, deren er doch verschiedene noch nach der Übersetzung der Zayre, gemacht, sich der alten Mode gänzlich entäussert'' (Lachmann Muncker IX, 347)

The Mournful Nuptials, the other probable source of *Der Schlaftrunk*, is that in both the English pieces a morose father opposes the match of his daughter In 1751, as has been mentioned, the dramatist had reviewed an abridged French version of Southerne's *Oroonoko*[75] Moreover, Southerne is named in the Prologue of *The London Merchant* as a prominent writer of domestic tragedy[76] If Lessing read Lillo's play at a time when he was keenly interested in domestic tragedy, he may have been led thereby to procure *The Fatal Marriage* (provided he had not already read Southerne's drama)[77] *A Woman Killed with Kindness* presumably was accessible to Lessing before 1755 It is to be found in Dodsley's *Select Collection of Old Plays* (London, 1744), a work cited by his friend Nicolai in an article written before August 31, 1756[78] This article, a historical account of early English drama, was later used as the first part of the "Geschichte der englischen Schaubuhne" (1758), published in Lessing's *Theatralische Bibliothek*[79] In the latter part of the "Geschichte," special mention is made of the fact that *A Woman Killed with Kindness* was published in Dodsley[80] For several years before October 1755, Lessing lived in Berlin, the home of Nicolai Inasmuch as Lessing's interest in the theory of domestic tragedy was particularly strong during the period of a year or more immediately preceding the production of *Miss Sara Sampson*, he may well have read at this time *A Yorkshire Tragedy, The Fatal Marriage*, and *A Woman Killed with Kindness*—as well as domestic tragedies not mentioned in this discussion[81]

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[75] Lachmann Muncker IV 261

[76] The Tragick Muse sublime delights to show
Princes distrest and Scenes of Royal Woe

Upon our Stage indeed with wish d Success
You ve sometimes seen her in a humbler Dress
Great only in Distress When she complains
In Southern s Rowe's or Otway's moving Strains
The Brilliant Drops that fall from each bright Eye
The absent Pomp with Brighter Jems supply
(London 1781)

[77] This comment applies also to Otway s *The Orphan* and Rowe s *The Fair Penitent*.

[78] Lachmann Munckner XIX 48

[79] *Ibid.*, n 1

[80] Deutsche National Litteratur edition V 353 For citations of Dodsley in the early portion of the article see pp 341 ff

[81] There is a curious identity in the names of a character in *Miss Sara Sampson*, Sir however, may be mere coincidence William and Sampson, though not occurring in con William Sampson, and of the author of *The Vow Breaker* (1636) William Sampson This junction, are both to be found in the sources from which Lessing took the names of all the other characters in his play

The evidence which has been discussed justifies the conclusion that in 1755 Lessing was well read in the English domestic tragedy produced between 1660 and his own time His comment on English domestic tragedy in the "Abhandlungen von dem weinerlichen oder rührenden Lustspiele," his extensive knowledge of Restoration and early eighteenth century English drama by 1755, and his later references to English domestic tragedies or to authors who produced examples of the genre—these points indicate that he must have had a rather thorough acquaintance with the field at the time of writing his own epoch-making play *Caelia* and *The Perjur'd Husband* are sources of *Miss Sara Sampson* (1755), *The Mournful Nuptials* seems to be connected with *Der Misogyn* (published 1755) and *Der Schlaftrunk* (begun 1766), other English domestic tragedies which he almost certainly knew are *The Orphan, The Fair Penitent, The London Merchant, The Gamester,* and *The Fatal Extravagance*

Miss Sara Sampson does not seem to have been influenced by the English domestic tragedies produced before 1660 These are chiefly murder plays, such as the anonymous *Arden of Feversham* (published 1592) and *A Yorkshire Tragedy* (published 1608) Several pieces—of which the most important is Heywood's *A Woman Killed with Kindness* (published 1607)—are much softer in tone, but they do not reach the degree of sentimentality of the typical eighteenth century English domestic tragedy and of Lessing's first *bürgerliches Trauerspiel*

The main domestic tragedies between 1660 and 1703 are Otway's *The Orphan* (1680), Southerne's *The Fatal Marriage* (1694), and Rowe's *The Fair Penitent* (1703) Though dealing with domestic situations rather than with political complications, these plays do not fully conform to Lessing's conception of the *bürgerliches Trauerspiel,* inasmuch as they treat the life of the nobility Moreover, they have foreign settings and are romantic in content Centlivre's *The Perjur'd Husband* (1700) is somewhat more realistic in spirit, but retains the social rank of the nobility and the foreign setting

The most important domestic tragedies between 1703 and 1755 are Hill's *The Fatal Extravagance* (1720), Lillo's *The London Merchant* (1731), Charles Johnson's *Caelia*[illegible] (1733), Lillo's *Fatal Curiosity*

[illegible] *Caelia* is not discussed in H W Singer's *Das bürgerliche Trauerspiel in England,* Leipzig, 1891

(1736), and Moore's *The Gamester* (1753) The special characteristics of these pieces are the treatment of English middle-class and common life in a more or less realistic manner, sentimentality, and excessive moralizing This is obviously the group to which *Miss Sara Sampson* belongs

The specific model of *Miss Sara Sampson* was *Caelia* First, as was mentioned above, Lessing used the Johnson drama as an important source Secondly, *Caelia* has the unique distinction of agreeing with *Miss Sara Sampson* in all essential characteristics The social settings of the two plays are exactly the same in each case the heroine is the daughter of a country gentleman, and the leading male character likewise belongs to the gentry Neither piece uses the judicial system for a final retribution,[63] both have sentimentality, excessive moralizing, and prose dialogue, and neither emphasizes religion On the other hand, all English domestic tragedies before 1755 except *Caelia, The London Merchant,* and *The Gamester* have verse dialogue *The London Merchant,* formerly regarded as Lessing's model differs from the German drama in having a mercantile setting, a legalistic basis (as have also *The Gamester* and many of the other English domestic tragedies before 1755), and a strong religious tone, the characteristics in which Lillo's work agrees with Lessing's—sentimentality, excessive moralizing, and prose dialogue—were rather conventional Incidentally, in structure *Miss Sara Sampson* likewise resembles *Caelia* rather than *The London Merchant* Whereas Lillo commences at the beginning of the series of events, the other two authors present on the stage only the very end of a long story Johnson permits but one night to intervene in the course of the drama, and Lessing limits the action to one day In short, though *Miss Sara Sampson* was presumably influenced as to type by many literary works—especially domestic tragedies, middle-class comedies (usually called "sentimental" comedies), and Richardson's novels—*Caelia* should be regarded as the German dramatist's pattern for the specific type of his own tragedy[64]

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[63] In Caelia, to be sure the heroine is arrested during the course of the drama, but the purpose (as in Richardson s Clarissa) is merely to heighten her distress Wronglove the villain, is not punished by the arm of the law

[64] For a more detailed discussion of Caelia as the specific model of Miss Sara Sampson, see MP, XXIV 85 90

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